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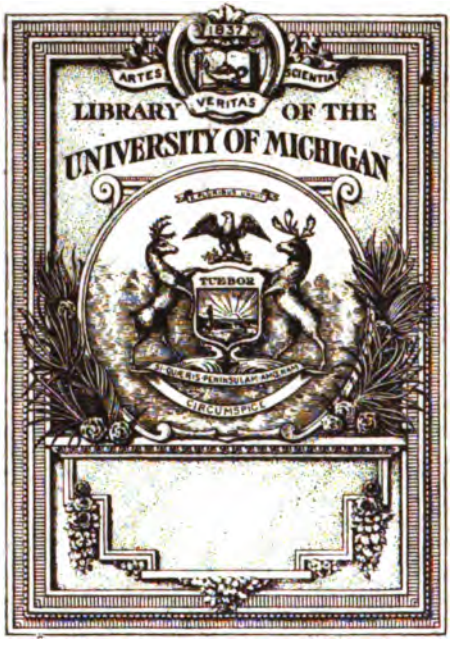

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Established 1897

Edited by

FORREST SHREVE

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THE THEORIES OF PHOTOSYNTHESIS IN THE LIGHT OF SOME NEW FACTS*

H. A. SPOEHR

Desert Laboratory, Tucson, Arizona

It is now more than one hundred and thirty-five years since the fundamental principles of the cosmical function of green plants was clearly recognized by Ingen-Houz, Priestley and Sénébier. The classical researches of de Saussure on the gaseous exchange of plants, which appeared shortly thereafter, still stand as the most thorough and masterly which have appeared in the history of the subject. Although the number of investigators who have worked on the problem of photosynthesis since the time de Saussure runs into the hundreds, and our knowledge of the chemistry of the substances involved in the process has been greatly extended, it cannot be claimed that we have as yet taken any decided step toward an understanding of the chemistry of the process based upon observation or rigid experiment.

However, the work of Sachs in the sixties, on the function of the chloroplasts, and the formation of starch therein, was the key to the chemical aspect of the problem, and served as a great stimulus to its further study. These researches established a direct relation between the carbon dioxide absorbed by the leaf and the starch formed therein. In fact, Sachs proved starch to be the first "distinctly recognizable" product in the process of photosynthesis. What then, is the course and sequence of chemical changes in the reduction of the simple compounds, carbon dioxide and water, to the highly complex starch?

With the developments of organic chemistry it was but natural that attempts should have been made to explain the mode of

*Substance of a paper read in the Symposium on Light Effects at the meeting of the Botanical Society of America at Leland Stanford University, August 4, 1915.

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reduction of carbon dioxide and the course of sugar synthesis in the green leaf. On the part of the chemist these attempts have been largely of a purely speculative nature, and some of the hypotheses proposed unfortunately show a lamentable lack of knowledge of the conditions under which photosynthesis takes place, as well as of the physiology and structure of the chlorophyllous cell. Probably largely for these reasons few of the suggestions offered by the chemists received any serious attention from the botanists, there being at the time few plants physiologists with sufficient training in or even sympathy with the chemical aspects of these problems.

The great success of the general method of synthesis in organic chemistry influenced the work in this field to a considerable extent, as is evidenced by the large number of attempts at extracellular photosynthesis. Some have fallen into the error of reasoning, that if they can produce sugar, or the substances closely related to sugar, from carbon dioxide and water, by almost any means, that this is necessarily also the process taking place in the leaf.

It can safely be said at the outset that, when critically considered from a physiological view point, none of the existing theories is even moderately well established by observation of facts.

The theory which in recent years has received most prominence is that suggested by Baeyer[1] in 1870. In a paper entitled "Ueber die Wasserentziehung und ihre Bedeutung für das Pflanzenleben und die Gährung," Baeyer discusses the various ways of splitting off of water and subsequent condensation of organic compounds. In 1861 Butlerow[2] had discovered that formaldehyde, in aqueous alkaline solution, condenses to an optically inactive syrup, possessing some of the properties of hexose sugars. Baeyer considers formaldehyde in aqueous solution to be $CH_2(OH)_2$ and that the Butlerow condensation is simply one

[1] Baeyer, A., Ueber die Wasserentziehung und ihre Bedeutung für das Pflanzenleben und die Gährung. Ber. deut. Chem. Ges. **3**: 63–78, 1870.

[2] Butlerow, A., Bildung einiger Zuckerarten durch Synthese. Ann. der Chem. (Liebig) **120**: 295–98, 1861.

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of water loss and condensation of six $CH_2(OH)_2$ molecules. $6\ CH_2(OH)_2 - 6H_2O \rightarrow COH{\cdot}(C(OH)H)4{\cdot}CH_2OH$.

Baeyer then suggests that this may be the way in which grape sugar is formed in the plant. The idea of the similarity of chlorophyll and haemoglobin was prevalent at the time; it seemed therefore likely that chlorophyll should also fix CO. The sunlight splits the CO_2 into CO and O, the oxygen escapes, and the carbon monoxide, held by the chlorophyll, is reduced to formaldehyde, $CO + H_2 \rightarrow COH_2$, which is then condensed to sugar. This is the substance of the Baeyer hypothesis, formulated without the support of experimental evidence, it was given as a mere suggestion. In recent years this hypothesis has largely directed the course of the investigations in this subject, and, it seems to the writer, to the detriment of critical and independent thinking on the broader aspects thereof.

The fact which more than any other gave strength to this theory, and which is the underlying principle of the whole idea, was the discovery of Butlerow. This discovery was elaborated by O. Loew,[3] who gave the name formose to the sugar mixture, and especially by Emil Fischer,[4] who prepared therefrom some of the sugars found in nature.

Although the conditions under which formose is formed from formaldehyde *in vitro* have been carefully worked out, this phase of the question has received no attention from the plant physiologists; we have no definite idea whether the conditions of solution in the chloroplasts are such under which condensation of formaldehyde takes place. We shall return to this subject later.

There are three main points which immediately arise on considering the Baeyer hypothesis, and the experiments that have been applied have been directed in these three different, though interrelated courses. From the very extensive nature of the subject some of the investigations have reached out far into other

[3] Loew, O., Ueber Bildung von Zuckerarten aus Formaldehyd. Ber. deut. Chem. Ges. **22**: 470–78, 1889.

[4] Fischer, Emil, Ueber die Verbindungen des Phenylhydrazins mit den Zuckerarten. Ber. deut. Chem. Ges. **21**: 988–91, 1888. Bildung von Acrose aus Formaldehyd. Ibid **22**: 359–60, 1889.

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branches of science, which are ordinarily but remotely connected with plant physiology. Although some of these studies have proved to have little application to the problem under consideration, there are, nevertheless, many results which may prove of great value. The three divisions referred to are:

1. The reduction of carbon dioxide to formaldehyde.
2. The detection of formaldehyde in illuminated green plants.
3. Experiments in which plants were given formaldehyde as the only source of carbon.

It may be of interest to review briefly some of the experiments which have been made in these three fields, and to discuss their physiological bearing.

A great variety of methods have been tried to reduce carbon dioxide. Ballo,[5] in 1884, got formic acid from carbonic acid by treating the aqueous solution with sodium or potassium. The attempts of Lieben[6] to ascertain the first reduction product of carbonic acid by the action of various reducing amalgams and nascent hydrogen, resulted in the formation of formic acid exclusively. In the various attempts that were made to reduce carbonic acid and its salts by electrolysis, formic acid was always the only product. Coehn and Jahn[7] also call attention to the interesting fact that the normal carbonates, and H_2CO_3 in the presence of acids, were not reduced, only the bicarbonates and the aqueous solution of CO_2 could be reduced. From this they conclude that neither the CO_3 ion nor the undissociated H_2CO_3 was reduced, but the HCO_3 ion. By the use of metallic magnesium Fenton[8] finally succeeded in reducing carbonic acid to formaldehyde, with formic acid as a probably intermediate step; he also showed that weak alkalies seem to aid materially in this reaction.

[5] Ballo, W., Ein Beitrag zur Pflanzenchemie. Ber. deut. Chem. Ges. **17**: 6–12, 1883.

[6] Lieben, H., Ueber Reduktion der Kohlensäure bei gewönlicher Temperatur. Monatsch. f. Chem. **16**: 211–47, 1895; **18**: 582–88, 1897.

[7] Coehn und Jahn, Ueber elektrolytische Reduktion der Kohlensäure. Ber. deut. Chem. Ges. **37**: 2836–48, 1904.

[8] Fenton, H. J. H., The Reduction of CO_2 to Formaldehyde in Water Solution. Jour. Chem. Soc. **91**: 687–94, 1907.

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Berthelot,[9] in 1864, suggested the dissociation of carbon dioxide into carbon monoxide and oxygen, $2\ CO_2 \rightarrow 2CO + O_2$, and a subsequent reduction of the CO, as the first step in photosynthesis. By means of the silent electric discharge Loeb[10] actually broke up CO_2 in this way, and has formulated an elaborate hypothesis of the photosynthetic process based on his experiments. Briefly, his results that are of interest here can be described as follows:

1. $2CO_2 \rightarrow 2CO + O_2$.
2. $CO + H_2O \rightarrow HCOOH$.
3. $CO + H_2O \rightarrow CO_2 + H_2$.
4. $H_2 + CO \rightarrow HCOH$.

Thus, by using something to take up the oxygen (as *e.g.*, chlorophyll solutions), Loeb obtained formaldehyde and formic acid, with ease and in quantity, from carbon dioxide and water by the use of the silent electric discharge. Of special interest is the fact that Loeb also noticed the formation of glycolyaldehyde from $2H_2 + 2CO \rightarrow CH_2OH{\cdot}CHO$. The further synthesis of the hexoses from glycolyaldehyde is a relatively simple matter. The basic principle in this scheme is the breaking down of CO_2 into CO and O_2, and the subsequent reduction of the CO. While from a chemical view point these observations are of great interest, the plant physiologist very naturally finds great difficulty in the application of these findings to the living plant as he knows it. The electrical conditions both in the plant and in the atmosphere surrounding it, have not been found to be of such a nature as to have their homologue in the currents used by Loeb. As yet we have no reliable data of a photoelectric effect which might transform the light energy into electrical energy in a manner that would bring about the above mentioned results. There is no evidence that in the photosynthetic process any wave lengths are utilized that lie outside of the visible portion of the spectrum, such as might be associated with the silent electric discharge, and to which Loeb ascribes the reducing action in his experiments. Furthermore, it is not without its importance that while Loeb

[9] Berthelot, M., Lecons sur les methodes général de synthése. Paris, 1864.

[10] Loeb, W., Zur Kentnis der Assimilation der Kohlensäure. Zeitschr. f. Elektrochem. **11**: 745–52, 1905; **12**: 282–312, 1906.

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dealt with gaseous carbon dioxide, it is practically certain that in the plant we are dealing with a substance of quite different properties, that is, carbon dioxide dissolved in water, carbonic acid or its salts.

Of a very similar nature are the recent experiments which have been carried out by the use of ultraviolet light from the quartz mercury vapor lamp. The results obtained by various investigators are, however, by no means congruous. Usher and Priestley[11] report that by exposing a saturated solution of carbon dioxide, in quartz tubes, to ultraviolet light they obtained "an easily recognizable quantity of formaldehyde, most of which was in the polymerized form." From this very simple experiment they conclude that "the primary products of photolysis of aqueous carbon dioxide are formaldehyde and H_2O_2, that the evolution of O_2 is due to the decomposition of the latter substance by catalase, and that up to this point the process is entirely non-vital, and can be reconstructed *in vitro*."

Berthelot and Gaudechon[12] found that CO_2 can be split into CO and O_2 by means of ultraviolet light, and that:

$$2H_2O \rightarrow 2H_2 + O_2. \text{ and}$$
$$CO + H_2 \rightarrow CH_2O.$$

They state that they were able to obtain formaldehyde from CO_2 only in the presence of hydrogen.

The recent experiments of Stoklasa[13] and his co-workers, with ultraviolet light have received a great deal of attention, and have, in fact, been quoted as finally establishing the formaldehyde theory of photosynthesis. For this reason these experi-

[11] Usher, F. L., and Priestley, J. H., The Mechanism of Carbon Assimilation. Proc. Roy. Soc. **84**: B. 101–12, 1911.

[12] Berthelot, D., and Gaudechon, H., Synthése photochimique des hydrates de carbon aux dépens des élements de l'anhydride carbonique et de la vapeur d'eau, en l'absence de chlorophyll; synthése potochemique des composes quarternaires. Comp. rend. **150**: 1690–3, 1910.

[13] Stoklasa, J., und Zdobnicky, W., Ueber photochemische Synthese der Kohlenhydrate aus CO_2 und H_2 in Anwesenheit von KOH, und in Abwesenheit von Chlorophyll. Monatsh. f. Chem. **32**: 53–75, 1911. Ueber die photochemische Synthese der Kohlenhydrate unter Einwirkung der Ultra-violetten Strahlen. Biochem. Zeitschr. **41**: 333–72, 1912.

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ments deserve a careful study; and a brief description of the experimental conditions and the chief conclusions follows. The reactions were carried out in a porcelain dish, placed in a desiccator which was covered with a sheet of mica, transparent to the ultraviolet rays. In the dish was placed the metallic alloy which, on the slow addition of a KOH solution, evolved hydrogen; carbon dioxide was passed through the solution in the dish; the quartz mercury vapor lamp was 5 cm. above the mica plate, and the gases passed through an opening in the wall of the desiccator, to be analyzed. Stoklasa states: Formaldehyde is not formed from carbon dioxide and water in ultraviolet light; only from carbon dioxide in the presence of potassium hydroxide and nascent hydrogen is formaldehyde formed by ultraviolet light; the nascent condition of the hydrogen is absolutely necessary. The action of nascent hydrogen on potassium bicarbonate produces formic acid even in the dark. Very evidently these results are not in accord with the statements of Usher and Priestley nor of Berthelot and Gaudechon. By the continued illumination of the mixture of CO_2 and KOH *i.e.*, potassium bicarbonate, and of the nascent hydrogen, formed by the action of the potassium hydroxide on the alloy, Stoklasa obtained a substance which possessed many of the properties of a hexose sugar, and whose phenylosozone compound gave a combustion analysis corresponding to a hexosozone. Based on these observations Stoklasa formulates his theory of sugar synthesis from carbon dioxide and water in the plant. The CO_2, taken in through the stomata, is converted into potassium carbonate and then to potassium bicarbonate. The latter substance "while being formed" is immediately reduced to formic acid, thus.

$$2KHCO_3 + \text{Light} \rightarrow K_2CO_3 + HCOOH + O$$
$$\text{Light} + H{\cdot}COOH \rightarrow HCOH + O.$$

The formaldehyde is then condensed to hexoses by means of the alkali. This is not the place to enter into a detailed discussion of the chemistry of Stoklasa's methods and results. There are, however, a few points of such vital importance to the problem under consideration that they cannot be passed by.

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As was found by the earlier workers, and noticed by Stoklasa himself, potassium bicarbonate is reduced to formic acid by nascent hydrogen in the dark. Hence there is no reason for assuming, that the formic acid in his experiments is a product of the action of the ultraviolet light. Again, Stoklasa concludes from the fact that formaldehyde plus oxygen in the light yields formic acid, that formic acid with hydrogen must yield formaldehyde. There are absolutely no experiments by Stoklasa or any one else to verify this latter statement. The writer may here be permitted to state that in connection with his experiments on the photolysis of certain plant acids, he has tried for the past three years to obtain formaldehyde from formic acid in the light, under a great variety of conditions of concentration, intensity of illumination, etc., but has never been able to accomplish this directly.

Passing on to the physiological discussion, the question immediately arises what is the source of the nascent hydrogen necessary for the reduction? The amount of hydrogen necessary under the Stoklasa theory is by no means insignificant, probably at least two volumes of hydrogen to one of carbon dioxide. Stoklasa[14] theoretically derives this hydrogen from the breaking down of sugars by glucolytic enzymes. While it is probable that some hydrogen is formed in this latter process, there is no evidence that hydrogen is formed in such quantities.

It can therefore be safely said, that as yet we have no clear record of a reduction of carbonic acid or its salts to formaldehyde which could be applied to the process going on in the leaf, and is compatible with our present conceptions of the conditions existing in the chlorophyllous cell.

Turning now to the second theme, the detection of formaldehyde in illuminated leaves: Curtius and Franzen,[15] report that they obtained formaldehyde from beech leaves by distillation with steam. Their methods of analysis, however, have been se-

[14] Stoklasa, J., und Zdobnicky, W., Ueber die Glukolytische Enzyme in den Pflanzenorganismen. Zeitschr. f. physiol. Chem. **50**: 303–60, 1907.

[15] Curtius, und Franzen, H., Die Chemische Bestandteile grüner Pflanzen. Ann. Chem. (Liebig) **390**: 89–121, 1912. Ibid, **404**: 93–130, 1914.

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verely criticised[16] as not giving reliable results. Pollacci,[17] also obtained aldehyde reactions in the distillate from illuminated leaves; these reactions were not obtained from leaves kept in the dark, without CO_2, nor from chlorophyll-free parts. The largest number of investigations have been made by means of microchemical methods, using the various color reactions as indication for the presence of formaldehyde. The difficulties of this method are undoubtedly very great, as in but very few cases are the tests sufficiently intense, so that it usually comes down to distinguishing between various shades and colors produced by other aldehydes and related substances present in the leaf. Nevertheless, Pollacci, Grafe, Kimpflin,[18] Gibson[19] and others have reported the presence of formaldehyde in illuminated leaves. However, recently it has been found that there are a number of substances present in the leaf which produce formaldehyde in the light quite independently of the reduction of carbon dioxide. Warner[20] has found that chlorophyll films, under the action of the oxygen of the air, produce formaldehyde in the light. So also, Wager[21] has shown that chlorophyll extracts, under the influence of light, yield formaldehyde, and that the bleaching of chlorophyll is not a result of the activities set up by photosynthesis as suggested by Usher and Priestley. This, of course, still admits the possibility that the carbon dioxide is taken into the chlorophyll molecule, which then by photolysis yields formaldehyde. The writer[22] has also found that a number of organic acids which are known to be very common components

[16] Fincke, H., Nachweis von Formaldehyd in den Pflanzen. Biochem. Zeitschr. **52**: 214–25, 1913.

[17] Pollacci, G., Intorno alla presenza dell aldeide formica nei vegetali. Atti del R. isti. bot. dell'univ. Pavia, **6**: 27, 1899. Atti Acad. dei Lincei, 1907.

[18] Kimpflin, G., Présence du menthal dans les végétaux vertes. Compt. rend. **144**: 148–50, 1907.

[19] Gibson, R. J. H., Photoelectric Theory of Photosynthesis. Ann. of Bot. **22**: 117–20, 1908.

[20] Warner, C. H., Formaldehyde as an Oxidation Product of Chlorophyll Extracts. Proc. Roy. Soc. **87**: B, 378–85, 1914.

[21] Wager, H., The Action of Light on Chlorophyll. Proc. Roy. Soc. **87**: B, 386–407, 1914.

[22] Spoehr, H. A., Photochemische Vorgänge bei der diurnalen Entsäurung der Succulenten. Biochem. Zeitschr. **57**: 95–111, 1913.

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of leaves, yield formaldehyde on exposure to the light. Formic acid, however, does not yield formaldehyde. In fact, it is not improbable that there are a large number of substances in the plant which produce formaldehyde under various conditions. Hence it is quite evident that the finding of formaldehyde in illuminated leaves is of little value in the proof of the Baeyer hypothesis.

As to the experiments in which formaldehyde was given plants as the only source of carbon, the results are also somewhat contradictory. Formaldehyde has always proved to produce decidedly toxic effects even in concentrations of 1 : 20,000; although Treboux[23] found that *Elodea* could well stand a solution of 0.001%, but formed no starch. Loew and Bokorny[24] found that the sodium bisulphite compound of formaldehyde is not only very much less toxic, but that from solutions of this compound, in the presence of mineral nutrients, starch is formed by several algae. It is very important to remember, however, that these solutions are always slightly alkaline, which would have the effect of condensing the formaldehyde to sugar, and thus that it is from this latter substance that the plant is producing starch. Recently Bokorny reported that *Spirogyra* formed starch from a 0.001% solution of formaldehyde, and that this action was greatly accelerated by the action of light. The necessity of light for the utilization of formaldehyde by the plant has been clearly shown in the experiments of Grafe.[25] He showed that only those portions of the plant bearing chlorophyll are not injuriously affected by the formaldehyde in the light. In darkness formaldehyde is toxic to all plant parts. However, in these experiments there was no formation of starch in the leaves of the plants used (*Phaseolus vulgaris*), due probably to the inhibiting action of formaldehyde on the amylase.

[23] Treboux, O., Einige stoffliche Einflüsse auf die Kohlensäure-assimilation bei submersen Pflanzen. Flora **92**: 49–76, 1903.

[24] Bokorny, T., Ueber Stärkebildung aus Formaldehyd. Ber. deut. Bot. Ges. **9**: 103–6, 1891. Archiv. für Ges. Physiol. **125**: 467–90, 1908. Ibid **128**: 565, 1909. Biochem. Zeitschr. **36**: 83–97, 1911.

[25] Grafe, V., Untersuchungen über das Verhalten grüner pflanzen zu gasförmigen Formaldehyd. Ber. deut. Bot. Ges. **27**: 19, 1909; **29**: 431, 1911.

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In a very carefully executed investigation, Miss Baker[26] has studied quantitatively the effect of formaldehyde on plants. She found that in the light formaldehyde is used for the synthesis of food material; "the gain in dry weight produced was about half the loss due to respiration, and an increase in the percentage of formaldehyde in the air did not produce a corresponding increase in dry weight after a certain concentration." The idea of Grafe that chlorophyll acts as a protection against formaldehyde poisoning was shown to be incorrect, and that it is only in the light that formaldehyde is not highly toxic. It was furthermore established that the formaldehyde has no influence on the respiration of the plant.

From the experiments of Bokorny, Grafe, and Miss Baker, it appears, therefore, that formaldehyde may function as a stage in the process of photosynthesis, or otherwise serve the plant as material from which food can be manufactured, but in order to do this light energy is necessary. This would introduce an entirely new phase in the theory of Baeyer.

A modification of the Baeyer theory which combines therewith some of the features of the old Liebig hypothesis has been advanced by Emil Baur.[27] He considers oxalic acid to be the first reduction product of carbonic acid, the former substance is then reduced to glycolic acid, which in turn on photolysis, yields formaldehyde. Baur arrived at this conclusion as the result of his photochemical studies in which he found that the reduction of carbonic acid to oxalic acid and then to formaldehyde, required one-third the energy of the direct reduction of carbonic acid to formaldehyde.

It may be of interest now to note here briefly the results of some of the experiments on various photochemical reactions bearing on photosynthesis, carried out by the writer within the last few years. Tucson has proved to be a most admirable place

[26] Baker, S. M., Quantitative Experiments on the Effects of Formaldehyde on Living Plants. Ann. of Bot. **27**: 411–42, 1913.

[27] Baur, Emil, Ueber die Genesis der Kohlenhydrate. Naturwissenschaften. **1**: 474–7, 1913. Zeitschr. physik. Chem. **63**: 683–710.

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for these investigations on account of the large per cent of clear days and the exceedingly high light intensity. A great number of experiments have been made with the object of reducing carbon dioxide by means of light from various sources.

In view of the contradictory results given by Usher and Priestley, Berthelot and Gaudechon and Stoklasa and his coworkers, it was thought important to try out the effect of ultraviolet light on carbonic acid and its salts. It was found that neither carbon dioxide as a gas with water vapor, nor CO_2 dissolved in water, in various experiments, exposed from one to one hundred and fifty hours, ever yielded tests for formaldehyde which were sufficiently distinct to definitely establish the presence of that substance. The tests employed for formaldehyde were:

1. Diphenylamine in concentrated sulphuric acid.[28]
2. 0.5% resorcin with concentrated sulphuric acid.[29]
3. 40% NaOH plus 5% resorcin.
4. Rosaniline in sulphurous acid plus hydrochloric acid.[30]

Instead of using a metallic alloy to produce nascent hydrogen, as Stoklasa had done, this was prepared electrolytically. A large quartz flask, partially filled with a $KHCO_3$ solution, and bearing a three-hole stopper was used. Through one hole passed a glass tube to the bottom of the flask for the supply of CO_2, this tube also carried the negative wire from a small electric generator, the wire was fastened to a platinum electrode from which the hydrogen was evolved at the bottom of the flask. The second hole was used for the electrolytic bridge: a glass tube, filled with K_2CO_3 solution, connecting with the solution in the flask and the other end with a dish of K_2CO_3 solution; in this dish was placed the positive pole of the generator. Through the third hole in the stopper passed a tube to carry off the gases from the flask to the cooled absorbing vessels. Thus, nascent hydrogen

[28] Grafe, V., Ost. bot. Zeitschr. **64**: 289–91, 1906.

[29] Abderhalden, E., Handbuch d. Biochem. Arbeitsmethoden. II, 15. Lebbin, Zum Nachweis d. Formaldehyds. Pharm. Ztg. **42**: 18, 1897.

[30] Fincke, H., Nachweis von Formaldehyd in den Pflanzen. Biochem. Zeitschr. **52**: 219, 1913.

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was constantly evolved in the flask, and by the combined action of the electrolysis of the $KHCO_3$ solution, and the CO_2 which was run into the flask, potassium bicarbonate was continuously being formed. These are the conditions which Stoklasa considered essential for the formation of formaldehyde. However, no formaldehyde was ever obtained.

It is important to note that in these experiments *formic acid* was found to be the only reduction product. Even without the nascent hydrogen an aqueous solution of carbon dioxide can be reduced to formic acid by exposure to ultraviolet light. Larger amounts of formic acid are formed from potassium bicarbonate, which is probably due to the fact that solutions of the latter salt contain a higher concentration of HCO_3 ions than does a solution of carbonic acid. In view of these facts, the old idea proposed by Erlenmeyer that formic acid may play an important rôle in the photosynthetic process gains new significance.

As was mentioned above repeated attempts have been made to obtain formaldehyde from formic acid by means of exposure to ultraviolet light and sunlight. Many of the plant acids do yield formaldehyde on being exposed even a short time to sunlight. However, it was never possible to detect a reduction of formic acid to formaldehyde. On the other hand, it has been possible to synthesize a sugar-like substance from formic acid by means of sunlight or ultraviolet light. When solutions of formic acid were exposed to sunlight or ultraviolet rays, for from ten to fifty hours, and the water was then distilled off, there remained a yellow, non-volatile syrup. This substance has many of the properties of a sugar—it reduces Fehling's solution as well as Tollen's solution. Algae develop in solutions thereof in the dark, so can evidently use the substance as a source of carbon. When oxidized with nitric acid, oxalic acid is formed therefrom.

Unfortunately the amount of this substance formed in any one experiment is not sufficiently large so that the necessary chemical investigations can be made. This is due to the fact that the action is reversible, that is, not only is the substance formed in the light, but light also easily decomposes it; so that what is finally obtained is the difference between these two actions proceeding

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in opposite directions. Thus far it has not been possible to discover conditions which favor only the synthetic action. In the light from a quartz mercury vapor lamp, both the synthetic and the decomposing actions are greater than in sunlight. It is an interesting fact that the photolysis of this syrup yields, besides formic acid, a volatile substance giving many of the tests for aldehyde. All that can be said at this time, however, is that this is not formaldehyde.

Attention has already been called to the fact that the basis of the Baeyer theory is the fact that the formaldehyde solutions are condensed to sugars by means of alkalies. It is important to consider the conditions under which this reaction takes place. From the very extensive researches of Nef[31] it is certain that the condensation of formaldehyde to sugar takes place only with alkali hydroxides and at high temperatures. Is, therefore, this reaction actually applicable to the plant?

It is true that the heat energy necessary in the *vitro* reaction might be obtained in the plant from the sunlight. But that the necessary concentrations of alkali exist in the plant seems very doubtful, and there is no evidence for assuming the presence of some unknown enzyme which might take the place of the alkali hydroxides. As to the action of the chloroplasts in this connection, we are equally without evidence. It seemed therefore not without interest to determine the action of sunlight on formaldehyde solutions in the presence of weak alkalies, such as might possibly exist in the plant, and at ordinary temperatures.

Three per cent formaldehyde solutions were used, with the salts in tenth normal concentration. These solutions, in glass flasks, were exposed directly to the sunlight. Calcium carbonate, potassium bicarbonate, basic magnesium carbonate, zinc carbonate, and potassium nitrate (which forms an alkaline solution in the sunlight),[32] after four months of insolation showed no trace of sugar formation. Lead hydroxide, calcium hydroxide and

[31] Nef, J. U., Dissociationsvorgänge in der Zuckergruppe. Ann. d. Chem. (Liebig) **403**: 355, 1913.

[32] Spoehr, H. A., The Relation between Photosynthesis of Carbon Dioxide and Nitrate Reduction. Science **23**: 63–4, 1911.

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potassium carbonate formed sugar in the dark as well as in the sunlight. It seems quite doubtful, therefore, that the condensation of formaldehyde to sugar can take place in the plant in the sense of the Butlerow reaction.

In the foregoing experiments it was noticed that the main reaction was the formation of formic acid from the formaldehyde. Even in neutral solution the formaldehyde was very readily oxidized in the sunlight.

It was furthermore established that formaldehyde vapor mixed with air is quickly oxidized to formic acid in the sunlight. In view of this fact the experiments of Grafe and of Miss Baker take on a very different aspect. The question immediately arises, were the plants in these experiments appropriating any formaldehyde at all, or was it the formic acid (formed by oxidization of formaldehyde in the sunlight) that served as a source of carbon; and is the phenomenon of the reduction of the toxicity of formaldehyde by light to be explained by the fact that this substance is converted into formic acid in the light?

I have studied the action of gaseous formic acid on green plants in the light, and have found that although this acid is quite toxic to the roots, the chlorophyllous portions develop normally in an atmosphere of formic acid, show an appreciable gain in dry weight, and also form starch.

In conclusion, some of the failings of the formaldehyde hypothesis, both from a chemical and physiological aspect have been pointed out, and an effort has been made to show that this hypothesis, though alluring on account of its simplicity, is by no means as well established as many writers on the subject would have us believe. This criticism has as its object not the overthrowing of ideas that have proved to be fruitful, but rather the urging of experimentation and observation, unfettered by hypotheses, on a subject that requires for its investigation the masterly application of many branches of science and the frank coöperation of the most skilled workers in these various fields.

It has been shown that carbon dioxide and water are easily reduced to formic acid by means of light, that from this latter

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substance a sugar-like syrup (analogous to formose) is formed under conditions such as exist in the plant leaf, that this substance can serve as the only source of carbon for the development of the plant, and finally, that plants thrive in an atmosphere of formic acid in the light. These are the same criteria that have been applied to the formaldehyde theory with perhaps even a little less success. Yet, it seems to the writer, that this does not justify the advancing of a "formic acid hypothesis," for there still is a great deal of evidence which indicates that photosynthesis in the chlorophyllous leaf is a process of great complexity, the chemistry of which is fully as involved as that of fermentation and enzymatic action.

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ON THE BEHAVIOR OF AN EXCISED BRANCH OF THE SAHUARO

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Large individuals of the giant cactus or Sahuaro, *Carnegiea gigantea*, have been removed from time to time from their desert home to various institutions and other places in the United States where they have continued to grow and bloom almost normally from year to year. The specimens at the New York Botanical Garden have been notably successful considering the changed relations which at best can scarcely approach the environic conditions which prevail within the natural range and habitat of this Papago-land xerophyte.

A curious but well known feature of these gigantic water-storage stems is seen in their ability to withstand desiccation and to produce flowers even though the greater bulk of the plant body may have been killed. MacDougal and the members of the staff at the Desert Laboratory have conducted extensive and intensive investigations upon the behavior of uprooted plants and of excised portions of the Sahuaro as well as of many other cacti and cactus associates. The "water-balance" of desert plants is a problem to which MacDougal has directed his attention for several years in connection with the numerous projects which are constantly under investigation by the Department of Botanical Research of the Carnegie Institution. In 1908 this writer called attention[1] to the fact that decay sometimes begins in the lower part of the main stem of the giant cactus and slowly proceeds upward. The fleshy cortex and pith of the main trunk go to pieces first and thus expose the rod-like units of the woody cylinder. In spite of the fact that the lower part of the stem is dead the upper branches may retain their normal form and color

[1] Across Papagueria. Plant World 11: 93–99, 1908.

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for many months. This condition presents a curious appearance with the top-heavy plant high in the air connected to the soil only by the naked skeleton below. Living green branches of this sort are reported to have maintained such an independent existence above the dead skeleton for as long as fourteen months.

The same author reported[2, 3] that in some cases such isolated branches which had had no water for a year have produced flowers. MacDougal considers that this phenomenon is in accord with many other observations that approaching dissolution often stimulates the reproductive processes.

In April, 1914, MacDougal superintended the collection of a branch of the Sahuaro and the shipment of the same from Tuscon to the department of botany at the University of Nebraska. The specimen was started from the desert on April 19 or 20 and reached Lincoln on April 27. The branch which had been neatly cut away from the main trunk was about 8 dcm. long, slightly curved and at the time of shipment was provided with several swelling flower buds. The behavior of this isolated branch is of interest in connection with previous studies of this species some of which have been briefly noted above.

The excised branch was carefully unpacked in the greenhouses of the department of botany in the presence of what Professor Bessey characterized as "an admiring throng." At that time it was noted that several of the larger flower buds had been injured in transit and had fallen off. However the branch still retained one large bud which appeared to be normal and which gave promise of opening within a few days. The branch with its single precious bud was erected in a large earthen flower pot and the lower part was covered with dry sand to a point well above the scarified end. The whole preparation was then placed upon the driest, sunniest, and hottest bench available in the greenhouses.

The first large bud opened early on the morning of May 5 and remained open only the one day since the weather was clear and warm and under these conditions it was found that the flowers

[2] The water-balance of desert plants. Ann. Bot. **26**: 71–95, 1910.

[3] The water-balance of succulent plants. Carneg. Inst. Wash. Pub., No. 141, 1910.

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Fig. 1. Flower on the excised branch of Sahuaro.

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are open for a single day or less. But this was probably the first time that the giant cactus ever bloomed in Nebraska. On May 17 three buds opened, and the day being Sunday the flowers were seen by many people who were delighted with the display.

After the second series of buds had opened we supposed that the branch was done producing flowers and we then centered our interest upon such questions as to how long the specimen would live, if new roots would be formed from the wound caused by cutting the branch off, etc., etc. Much to our surprise, however, in a few days we noted that additional buds were appearing and evidently we were to see still more flowers. One of these buds opened on May 27 and another on May 28 after which no flowers were produced until June 28 when another normal bud opened. After a flowering period of almost two months we concluded that the flower of June 28 was surely the last but imagine our surprise when on September 18 one more flower appeared. This closed flower production on the excised branch for 1914. Seven flowers had opened but in all cases the ovaries withered and fell from the plant and not one ripe fruit developed. Artificial pollination was resorted to but even this did not result in the growth of the ovary even until the perianth segments were thoroughly collapsed.

The structure of the flower of *Carnegiea* is well known to everyone. The great number of stamens is especially noteworthy. Bessey[4] has already reported that in one of the flowers produced by this isolated branch there were 3482 stamens and 1980 ovules by actual count.

We were now quite sure that no more flowers would be produced during the season of 1914 so we began to direct our study to other features of the potted branch. About October 15 the branch was removed from the container, the lower end was dusted off and carefully examined for the appearance of roots. The wound by this time had become thoroughly covered with a soft spongy callus but no signs of roots could be found at any point. The callus was practically continuous. Decay had not appeared in any degree whatever.

[4] Science, N. S., **50**: 680, 1914.

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The branch was watched closely with the approach of the growing season of 1915 in order to notice the slightest evidence of renewed activity. Our vigilance was rewarded when early in May numerous flower buds began to push out from the upper portions of the cortical ridges. To our surprise the buds were formed in greater numbers than in 1914 and their rate of growth was much accelerated. This is probably accounted for by the fact that May, 1915, was a rather warm and clear month at Lincoln. These buds began opening on May 12 and for the following ten to twelve days there was scarcely a day when there was not at least one flower open. As many as five flowers were open on one day. Blooming came to a close on May 22 after the production of thirty-two flowers and eight or ten aborted buds. No fruits were set by any of these flowers and no flowers were produced after this first burst of bloom from May 12 to 22.

So intense was the interest in the flower production of the excised branch that it was rather late before anyone thought of the desirability of taking the weight of the branch from time to time. This was done for the first time on September 30 after the close of the first flowering period. Further weighings have been made at intervals since that time but these data are not yet ready for publication.

A second branch similar to the above was sent to us from the Desert Laboratory in the autumn of 1914. This branch was treated like the first one but it did not produce flowers or buds in the spring of 1915. When our landscape gardener was planting the cactus bed upon the campus for the present summer we decided to place this last specimen in the soil out of doors with the rest of our cacti, all of which have invariably made very satisfactory progress outside of the plant house during the summer. Heavy rains set in soon after the planting was done with the result that the cut branch of the giant cactus began to rot at the lower end. The progress of decay was so exceedingly rapid after it was first discovered that we scarcely had time to remove the branch from the out-of-door bed to the laboratory and cut it into pieces in order to save some of the normal tissues for histological study. The experiment proved conclusively

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that to plant excised branches of the giant cactus out-of-doors in the rather heavy loam of the corn belt is a very unwise practice, especially during a rather abnormally moist season.

The living green branch still appears to be perfectly normal and has been kept in dry sand in the greenhouse and has been weighed from time to time during the current year. This branch was examined for roots a second time on May 30, 1915, and again on July 28 but none were to be seen. The end of the branch is now thoroughly covered with a thick layer of dry cork and apparently no roots are to be formed. The plant is in excellent condition so far as external symptoms go, although it is getting no water. At this time (July 31, 1915) we can only wonder how much longer the branch will live and if we will see a third post-excision period of flower production in 1916.

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BOOKS AND CURRENT LITERATURE

REPORT OF THE SELBY SMELTER COMMISSION.—This Commission, appointed by agreement between litigants in the California courts to examine into alleged agricultural and other injuries produced by smoke from the Selby Smelter, near San Francisco, made its report in November, 1914, and the report has now been published in full by the U. S. Bureau of Mines.[1] Many of the data presented are of local application only but certain features have general interest and some of these are important to botanists. Of special interest are the extensive and thorough studies of the effect of sulphur dioxide on barley plants conducted by Mr. A. E. Wells, Metallurgist and Chief Chemist of the Commission, and reported on pages 213 to 307 of the Bulletin cited. There is a brief summary of this work with the conclusions of the Commission on pages 39 to 46. Experiments were conducted in the field at two localities in California and a total of 141 plots 20 by 4 feet in area and containing barley plants growing under field conditions were subjected to fumigations with air carrying known amounts of sulphur dioxide between 1 part and 20 parts per million. The action on the plants, if any, was judged by visible injury and by the effect on the yield.

It was found that the occurrence and severity of injury is determined mainly by three factors: the concentration of the sulphur dioxide in the air, the length of time during which it is applied, and the humidity. When the time between applications was short, intermittent application produced practically the same effect as continuous application for the same total time. When the time between applications was relatively long the effect of intermittent application was less severe than that of continuous application. For the same concentration and time of application injury is greater the higher the humidity. There are innumerable combinations of concentration, time of application and humidity which will produce injury. The "toxic limit" of concentration must be defined with relation to both of the other factors. The Commission believes it possible to produce injury by the continu-

[1] Bureau of Mines, Bulletin 98, 520 pp. 1915. The Commissioners were the late Dr. J. A. Holmes, Dr. Edward C. Franklin of Stanford University and Mr. Ralph A. Gould, of San Francisco.

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ous application under conditions of high humidity of so small a concentration as 0.5 part of sulphur dioxide per million of air. Under ordinary humidity conditions 20 parts per million produced severe injury in 15 minutes; 10 parts per million produced injury in 30 minutes; and 5 parts per million produced injury in an hour. Injury could be produced by 2 parts per million applied for 4 hours continuously or for 10 minutes daily during the entire growing season (10 to 12 weeks). With 1 part per million slight visible injury was produced by two 7-hour fumigations but a total of six 7-hour fumigations or ninety 10-minute fumigations did not decrease the yield.

The concentrations found by the Commission to be injurious were surprisingly low and far below the concentrations reported by previous investigators as the lowest capable of producing injury. This discrepancy is explained as due to the fact that previous investigations have been made by introducing the measured amount of sulphur dioxide into a closed space containing the plant to be tested. In the Commission's experiments the atmosphere was moved through the test chamber and was maintained at the proper concentration. It appears that there is a marked absorption of the sulphur dioxide both by the plant tissues and by the soil[2] and it is probable that the earlier investigators had in their containers far lower atmospheric concentrations of sulphur dioxide than they supposed to be present. Both this absorption of sulphur dioxide by the plant and the results of widely separated intermittent fumigations suggest that the injury is really determined by the balance of two rates; the rate at which sulphur dioxide is absorbed by the plant, and the rate at which it is removed by physiological processes, given off again to the atmosphere or otherwise disposed of. Doubtless both of these rates are affected by many factors, some of which are undoubtedly internal to the plant. It is easy to understand the discrepancies in the work of previous investigators and to see why the determination of a definite concentration limit for toxicity has proved impossible.

The Commission's experts were unable to establish the reality of the so-called "invisible injury," a hypothetical decrease of yield supposed to be due to a toxic effect too slight to produce visible lesions. Apparently no decrease of yield occurs without easily visible injury existing or having existed. Indeed in several cases slight visible injury was observed but was followed by no decrease of yield.

[2] This was confirmed by collateral laboratory investigations by G. C. Bartells, Jr., reported on pp. 308–323.

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Unconnected with sulphur dioxide injury but of general interest is the discovery of the Commission's agronomists[3] that small quantities of both lead and arsenic are of normal occurrence in the soils of the region and in certain other California soils. The amounts found and not believed due in any degree to contamination from the Smelter, range from 0 to 10.0 parts per million of lead and from 0.2 to 8.0 parts per million of arsenic. These amounts are believed far too small to have significant agricultural effect, in which conclusion an attached statement of Prof. Charles B. Lipman agrees. The delicate analytical methods necessary to the investigation are described and there is a brief review of the literature of the occurrence of lead and arsenic in soils. Elsewhere in the report analytical methods are described for arsenic and lead in plants and in air dust and for sulphur in plants, also very careful and accurate methods for the determination of sulphur dioxide in air. There is also a series of experiments on the perception by man of small amounts of sulphur dioxide in the atmosphere. Of 60 persons tested nearly all could detect 4 parts per million of the gas and most of those previously acquainted with its odor could detect 3 parts per million. No one detected 1 part per million. Appended to the report is an annotated bibliography of 96 titles covering the effect of sulphur dioxide on vegetation and animal life.—E. E. Free.

[3] Charles F. Shaw and E. E. Free, pp. 454–462.

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NOTES AND COMMENT

Nine months ago two prizes were offered by THE PLANT WORLD for the best papers on any subject connected with the water relations of plants. The term for the submitting of papers closed on December 1 without any manuscripts having been received for competition. Are we to take it from this that the investigation of water relations is an unpopular subject and held in slight regard, or merely that the monetary morsel which we offered was too small to tempt our colleagues? We have more recently offered two prizes for papers in soil physics, to be submitted before December 1, 1916. We sincerely trust that this offer will not result in a complete abeyance of work in that subject during the year.

Dr. Herman E. Hasse, well known as a student of the lichens, died on October 29, 1915, at the Soldiers' Home, at Santa Monica, California, within a few months of his eightieth year. He was a native of Freiburg, Saxony, whence he emigrated with his parents at the age of nine. His training in medicine was begun in St. Louis, continued at Leipzig, and Prag, and completed at Wurzburg, where he received his degree in 1861. On returning to America Dr. Hasse served throughout the Civil War as a surgeon in the Ninth Wisconsin Volunteer Infantry. At the close of the war he practiced in Milwaukee, Arkansas and Missouri, and in 1885 settled in Los Angeles. From 1888 until 1905 he was chief surgeon to the Soldiers' Home. Dr. Hasse was an authority on the lichens of the Pacific Coast, and a long series of papers on this group are to be found under his name in the Bulletin of the Southern California Academy of Sciences. His best known work was the comprehensive treatise on "The Lichen Flora of Southern California," published by the Smithsonian Institution in 1913. Dr. Hasse was also a diligent student and collector of the higher plants, and his interest is commemorated in the genus *Hasseanthus*, dedicated to him by Dr. Rose. His thorough work as a pioneer in the botany of southern California, and the high esteem in which he was held by his friends and associates will long keep his memory fresh.—FORDYCE GRINNELL, JR.

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The Plant World

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THE GEOLOGICAL HISTORY OF GYMNOSPERMS*

EDWARD WILBER BERRY

The Johns Hopkins University, Baltimore, Md.

There are two considerations that I desire to emphasize before attempting to sketch the geological history of gymnosperms. These are (1) the vast period of earth history that had elapsed before any recognizable traces of vascular plants are found in the record, and (2) the reasons why they have not yet been found in the earlier Paleozoic periods. One is apt to speak of the Paleozoic flora as if it were an entity comparable to the recent flora although the Permian gymnosperms were separated from their known Devonian ancestors by a far greater interval than separates the existing flora from pre-glacial floras. A chronology is then one of the most important factors in any understanding of the succession of floras that have clothed the earth.

There are a great many ways of estimating geological time, most of them dependent on the comparisons of past processes with present processes, and all nothing more than approximations. It is possible, however, to get an idea of the relative durations of the different periods that will be reasonably accurate. Geologists segregate the rocks of the earth's crust, into five systems—Archeozoic, Proterozoic, Paleozoic, Mesozoic and Cenozoic. If 5 be taken to represent the duration of the Cenozoic then the Mesozoic will be represented by 12, the Paleozoic by 27, the Proterozoic by 27 and the Archeozoic by 30. Some idea of the vastness that these figures represent may be gained from the statement that the Swiss Alps, Himalayas, Pyrenees, and Rockies have been elevated and the Colorado Cañon eroded since the dawn of the Cenozoic; and neither mammals nor angiosperms are found as far back as the beginning of the Mesozoic.

* Paper read in the Symposium on Gymnosperms at the meeting of the Botanical Society of America at the University of California, August 3, 1915.

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The first land-plants known occur in the Devonian, which is only midway back in the Paleozoic, and the first invertebrate faunas of any representative character occur in the earliest Paleozoic.

From the figures of ratios given above it is seen that over half of geologic time had elapsed before any recognizable animals or plants are found. This explains the relatively high degree of organization of the earliest known fossils, both animal and vegetable, since more time intervenes between the formation of the earliest recognizable Archeozoic rocks and the appearance of fossil plants in the known record, than intervenes between that time and the present. This situation really holds out the hope that any day we may discover some unmetamorphosed lens of shale in these older rocks that will reveal to us the life of the ages long antecedent to the Cambrian.

From the high organization and consequent differentiation of the earliest known floras and faunas it is a legitimate conclusion that their ancestors passed through a long antecedent period of evolution. Terrestrial plant life in the oldest records comprises representatives of five phyla of vascular plants,[1] including seed-plants, so that the lost interval represents a longer period of evolutionary activity than the known record down to the present, thus confirming the evidences of chronology derived from physical sources.

The bulk of the early sediments have been many times subjected to the action of epeirogenic and orogenic forces and are consequently so altered that all traces of contained organisms have been obliterated. Moreover terrestrial plants are almost invariably preserved in lacustrine, fluviatile, or palustrine deposits on the bosoms of the continents or in the estuary and lagoon deposits of the continental margins. True marine deposits of whatever age rarely contain plants except such as contributed to the sea-drift and these are relatively few in number and usually unrecognizable by the time they were buried.

[1] The Pteridophyta or ferns, the Lepidophyta or lepidodendrons and sigillarias, the Arthrophyta or calamites and their allies, the Pteridospermophyta or seed-ferns, and the Coniferophyta or conifers.

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Both the deposits formed on the surfaces of the continents and those formed along their margins are the first to be destroyed in subsequent cycles of erosion, of which there have been many. Such types of sediments form a relatively small per cent of the geological column. The earliest unmistakable deposits of this sort known are in the Devonian and these do contain the remains of a complex terrestrial flora. In the following pages I have used the term "gymnosperm" in a morphological and not a taxonomic sense for there are serious objections to including in a single phylum all those very diverse plants that agree in possessing a micropylar canal.

PALEOZOIC HISTORY

Botanical literature abounds with discussions of the origin and mutual relations of the gymnosperms. The older views were based for the most part on the reproductive organs of the existing species while the later interpretations lean heavily on vascular anatomy, and both are highly speculative and have led equally competent students in quite opposite directions.

We all seem to share to a more or less degree that human tendency to consider only certain structures and not the totality of structures. Within my recollection the morphology of the higher plants was simply the morphology of floral parts as it is largely to this day. The monumental system of Engler and Prantl is based almost entirely on the morphology of what might properly be called the accessory reproductive organs. There is a devoutly held tradition among botanists that the reproductive organs are the most conservative of all organs and therefore merit most consideration. *A priori* I would consider them as more subject to evolutionary change than almost any other part of the plant and much less conservative than, for example, vascular structures or even foliar characters. Geologic history, it seems to me, fully confirms this assumption. A few examples will make this clear. Heterospory has arisen independently in nearly all the great groups. Its logical sequel—the seed habit, has also been acquired in unrelated lines, *e.g.*, in the great group of Lepidophytes which culminated in Paleozoic times, *Lepido-*

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carpon and *Miadesmia* are almost as far advanced in the seed habit as the contemporaneous Pteridosperms. Among the Pteridosperms we have the typical filicalian foliage, both in form and structure, surviving the change from homospory through heterospory to seed formation. Among the cycadophytes we find the foliage assuming the existing form in the Carboniferous and continuing unchanged throughout the ages during which the plants passed through the series of vascular and floral changes represented by the Mesozoic Cycadeoidales (Bennettitales) and Williamsoniales and the modern Cycadales.

Are the gymnosperms in the widest sense of the term monophyletic or polyphyletic? It seems to me that this is a question of degree rather than kind. Obviously if evolution is true we only have to go back far enough to find common ancestors. In the sense that none of the forms classed as gymnosperms are genetically related except in the remotest way to the group including the Lycopods and their Paleozoic relatives (which group may properly be called the phylum Lepidophyta) or to the group including the equiseta and their Paleozoic relatives (which group may be properly be called the phylum Arthrophyta) the gymnosperms are certainly monophyletic.

In another sense they may with propriety be considered polyphyletic and for the following reasons: The Paleozoic Pteridosperms while they grade off into little known forms of quite unsuspected structural possibilities, exhibit in those forms that are better known a sum of characters which precludes them from forming an order in a single taxonomic group that shall be termed Gymnospermae, and it seems to me that they are appropriately to be considered a separate phylum—the Pteridospermophyta, as suggested by Ward. Their sole coniferous character is the micropylar avenue of fertilization, a quite necessary stage in the evolution of the seed habit, as is proved by *Lepidocarpon* and *Miadesmia* among the Lepidophyta. It is true that the Pteridosperms do clearly indicate the character of the ancestral stock that leads to existing cycads, but they are probably not directly related, and in the latter we have another group, enormously diversified during the Mesozoic, one which in the judg-

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ment of many students is also entitled to rank as a phylum under the name of Cycadophyta as suggested by Nathorst. There remain four groups commonly considered as orders and probably of independent fern ancestry: (1) the Paleozoic Cordaitales, (2) the rather circumscribed Ginkgoales, which ranged from the late Paleozoic to the Recent, and enjoyed a considerable adaptive radiation during the Mesozoic, (3) the Gnetales, which Lignier would consider angiosperms, and which Wieland would apparently derive from the cycad alliance, and which may be passed over because they have no known fossil representatives, and (4) the Coniferales. These four groups, or at least the first two and the last, should be united in a larger unit of phyletic rank for which the term Coniferophyta proposed by Coulter may suffice.

The oldest known floras, those of the middle and later Paleozoic, contain two very distinct and yet not entirely unrelated types of gymnosperms—the Pteridospermae or seed ferns and the Cordaitales.

The Pteridospermae are the more primitive of the two and show every evidence of fern ancestry. Their stems were known for a generation or more before the detached fronds and seeds were correlated with them, and these stems because of their synthetic morphological characters were long known as Cycadofilicales. The Seed Ferns had foliage that was entirely fern-like in form and habit, as for example in the Sphenopteris type, which was highly decompound. These fern-like fronds had always been considered to be those of ferns although Stur as long ago as 1883 had suggested that they might be cycadaceous. The seeds were large and complex but were borne on fronds that were but slightly modified from the ordinary vegetative type and the pollen was borne in what might well be termed synangia on similarly unmodified fronds. Throughout the whole group nothing approaching cones is known, and the anatomy of stem or leaf, or both, was of the fern type. There was naturally great diversity of detail in this large plexus of forms and some are much more fully known than others.

At the present time at least a dozen genera based on stem

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anatomy and segregated into five families, are referred to the Pteridospermae (*Cladoxylon, Volkelia, Lyginodendron, Heterangium, Megaloxylon, Calamopitys, Medullosa, Sutcliffia, Steloxylon, Cycadoxylon, Ptychoxylon, Protopitys*). The fern like fronds involved in this group with their corresponding seed forms are as follows:

Sphenopteris—Lagenostoma
Neuropteris—Rhabdocarpus (in part)
Alethopteris—Pachytesta
Odontopteris—Odontopterocarpus
Linopteris—Trigonocarpus (in part)
Callipteris—Carpolithus (in part)
Callipteridium—Tripterospermum
Doleropteris—Codonospermum
Aneimites—Wardia
Dicksonites—Carpolithus (in part)

According to Scott, the Pteridosperms exhibit two lines of evolution,—one toward polystely, which becomes elaborated (Medullosaceae) and then extinct; and another in which a single stele becomes elaborated (Lyginodendraceae), the latter type is considered as approaching the Cycadophytes. According to Chodat, *Lyginodendron* is a specialized fern, an end product not concerned with cycad ancestry, which group originated from the Medullosaceae (which he renames Protocycadaceae).

We know too few members of what was really a great group to be dogmatic, but there can be no question but that our whole conception of Paleozoic floras and ancestral seed plants has been profoundly altered by what has thus far been demonstrated.

The other great group of Paleozoic gymnosperms, exemplified by the genus *Cordaites*, while they also show in their structure the evidences of a fern ancestry, had travelled the evolutionary road much farther than the Pteridosperms. They had lost all of the more obvious fern characters and were tall trees with a thick cylinder of secondary wood (*Dadoxylon*) of the araucarian type, differing from modern conifers merely in their larger pith. Their foliage consisted of a dense crown of spirally arranged, invariably simple and elongated, and sometimes very large leaves. The fructifications were small catkin-like cones, the ♂ and ♀ separate as in modern conifers. The cones were small, with thick spirally bracteate axes, in the one case bearing microsporophylls, and except for the bracts comparable to *Ginkgo;* and in the other case bearing short-stalked ovules. The pollen

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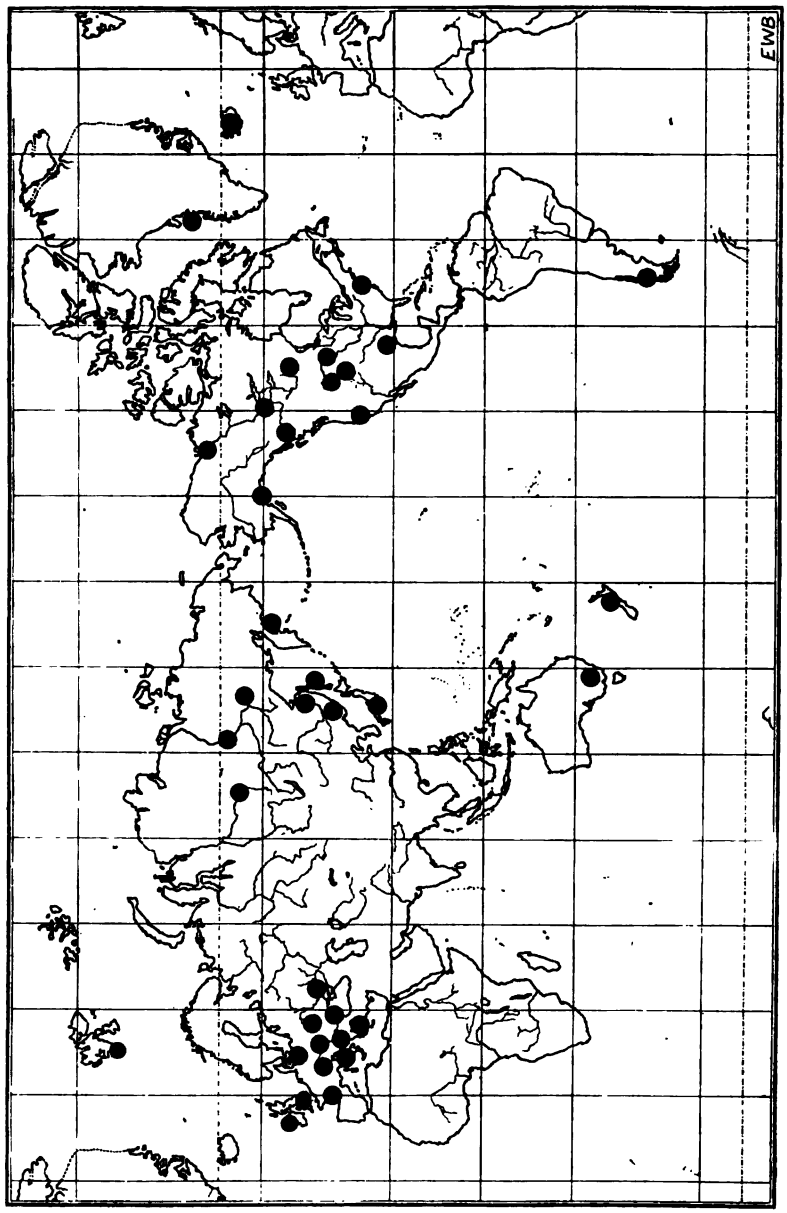

Fig. 1. Sketch map showing the location of Cenozoic records of *Sequoia*.

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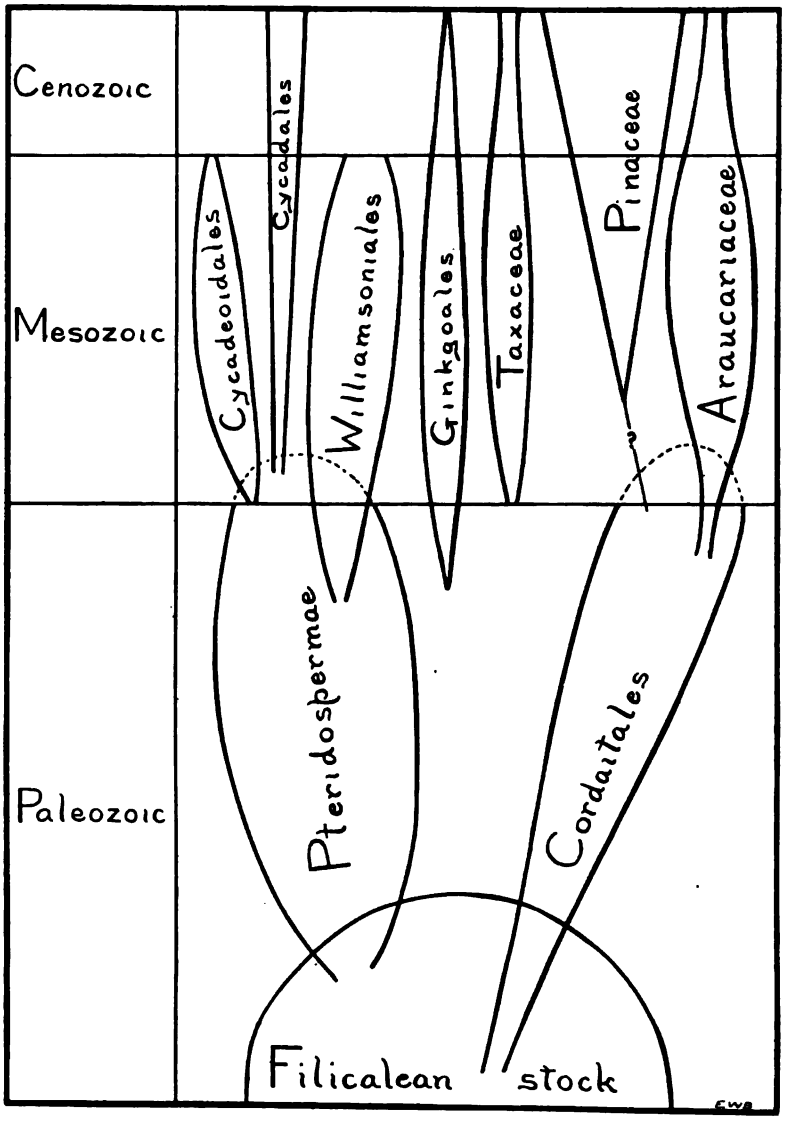

Fig. 2. Diagram showing the filiation and geologic history of gymnosperms.

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grains continued to grow after leaving the microsporangia and showed a group of prothallial cells or antheridium which developed motile sperms directly and without the formation of a pollen tube. The seeds were bilaterally symmetrical and usually winged.

Although we know *Cordaites* in detail, the impressions of foliage indicate that it constituted a large and diversified genus. Other types are known from fragments showing stem anatomy (*Pitys*, *Poroxylon*, *Mesoxylon*, *Callixylon*, *Caenoxylon*, *Mesopitys*, *Parapitys*, etc.) and it is quite possible that the *Ginkgo* line diverged from somewhere in the Cordaitean plexus in the late Paleozoic.

Both the Pteridosperm and the Cordaites stocks are known from the Devonian: Both were dominant groups that became cosmopolitan in the Carboniferous: Both continue in the Permian and neither is certainly known from the Mesozoic although a few stragglers may have lingered on into that era.

Three additional types of gymnosperms appear in the late Paleozoic record but as our knowledge of both is based largely upon impressions of the foliage little is known of their exact affinities. These three groups are the Cycadophyta, the Araucariaceae and the Ginkgoales, all of which became greatly differentiated and common during the Mesozoic. The genus *Psygmophyllum* of the Devonian Carboniferous and Permian is supposed to represent the Ginkgoales as is also the genus *Whittleseya* of the Carboniferous. In the Permian a considerable number of Ginkgo-like forms are known (*Ginkgophyllum*, *Baiera*, *Saportaea*, etc.). The araucariaceae are represented in the Upper Carboniferous by *Walchia* and *Schizodendron* and in the Permian by *Walchia*, *Ulmannia* and *Gomphostrobus*.[2] The cycadophytes appear to be represented as early as the Carboniferous by fronds of *Plagiozamites* and *Pterophyllum*, and the genus *Sphenozamites* is added in the Permian, but all of these types are infrequent until the next era.

[2] The genus *Voltzia* of the Permian is often considered as representing the Taxodieae.

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MESOZOIC HISTORY

The Mesozoic era has been called the age of conifers, and not without reason. The gymnosperms are represented during this time by five great groups—the Williamsoniales, Cycadales and Cycadeoidales (Bennettitales) of the cycadophyte phylum, and by the Ginkgoales and Coniferales of the Coniferophyte phylum. Of these five groups the Williamsoniales and Cycadeoidales appear to be limited to the Mesozoic: the Ginkgoales became practically extinct during the succeeding era: and there are a large variety of peculiar Mesozoic types of Coniferales.

Cycadophyta

It is but a few years since the Mesozoic cycadophytes, so abundantly represented by foliage in all parts of the world from the Arctic to the Antarctic, were generally accepted as representing true coniferous and carpellary-leaf bearing cycads not far removed from existing types. Then came the discoveries of Carruthers, Solms-Laubach, and especially Wieland, demonstrating the existence of forms in vegetative habit and appearance wholly cycadean, but with fructifications unique among gymnosperms. The sporophylls, instead of being solitary and terminal, were borne in abundance on lateral dwarfed branches among the leaf-bases, and were bisporangiate, suggesting comparisons with Ranalian flowers such as those of *Liriodendron* or *Magnolia*.

These forms are properly referable to the genus Cycadeoidea although many students abroad prefer the later name of Bennettites. These spectacular discoveries have resulted in a vast amount of misapprehension among botanists, who assume that the bulk of the Mesozoic cycadophytes were of this type, whereas it now seems clear that the Cycadeoidales were simply a bizarre side-line, stereotyped early in the Mesozoic, and without issue. Their great importance rests in the fact that because of their silicification at a number of localities they have furnished the key to the interpretation of the much more abundant and plastic group—the Williamsoniales. In these latter are represented a vast plexus of forms showing great variations in size, foliage,

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branching, and sporophyll structure. Their stems were prevailingly slender. Their fronds, of which innumerable genera and species have been described from all parts of the world, are among others the following types: *Ptilophyllum*, *Zamites*, *Otozamites*, *Sphenozamites*, *Glossozamites*, *Sewardia*, *Dictyozamites*, some *Podozamites*, *Wielandiella*, *Nilsonia*, *Pterophyllum*, *Dioonites*, etc.

The fructifications, which were the basis for the establishment of the genus *Williamsonia* long before their botanical affinity was known, were borne on an extended bracteate peduncle which is interpreted as a continuation of the slender stems but which may sometimes have been a lateral branch. These sporophylls consist of an ovulate receptacle much like that of Cycadeoidea surrounded by a whorl of microsporophylls that are much more reduced than in Cycadeoidea. These form a fairly well defined reduction series illustrated by the genera *Cycadocephalus*, *Weltrichia*, *Williamsonia*, and *Wielandiella*. Some are unisporangiate and are thought to be whorls from the cones of either monoecious or dioecious forms. For the details of the structure and relationships of these forms the reader must be referred to the recent literature on the subject.

The evidence for the existence of Mesozoic Cycadales of the modern type is decisive enough, but since the evidence of the fossil fronds has been invalidated by the discovery that they may represent any of the cycadophyte orders it seems probable that the Cycadales themselves were never an extensive group. The evidence for their existence in the Mesozoic rests on fossil carpellary leaves of the Cycas type in the lower Jurassic and on Zamia-like cones in the upper Triassic.

Coniferophyta

The Ginkgoales were abundant during the Mesozoic, but the differentiations were mainly of specific rank and very few variations of even generic rank occur. The two main types known—*Ginkgo* and *Baiera*—were much alike in fructifications and differed chiefly in foliage, the former with long petioles and the

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latter with short petioles and dichotomously inciso-partite lamina, with narrow linear segments. Both were cosmopolitan during the Mesozoic and *Baiera* appears not to have survived into the Cenozoic although *Ginkgo* was very common in certain regions during the latter era.

Of the three families of Coniferales (Araucariaceae, Taxaceae and Pinaceae) the Araucariaceae present more well marked features both anatomically and in sporophyll and foliar morphology than the other two. The fossil material comprises petrified wood, pith-casts, impressions of twigs, leaves, cones, cone-scales and seeds. Several Paleozoic genera have already been mentioned. In the Mesozoic this family was exceedingly common all over the world and included forms almost identical with the existing *Araucaria* and *Dammara* as well as a variety of other types. Thus along with the single seeded ligulate forms are others with a pair of seeds to the scale (*Pseudoaraucaria*), and others that were three seeded (*Protodammara*). *Araucaria* has been recorded in the Mesozoic from Spitzbergen on the north to Louis Phillipe Land on the south; from numerous localities in North America, Europe and Asia; and from scattered localities in South America, Africa and Australia. The most abundant forms in the Upper Cretaceous of the Atlantic Coastal plain from New Jersey to Alabama are leafy twigs and cone-scales of the *Araucaria Bidwelli* type, and *Dammara* cone-scales are found from Greenland to Texas, and in Europe as well. A considerable number of genera of Araucariaceae are represented in the Mesozoic of which the best known are perhaps *Pagiophyllum* and *Geinitzia*.

The family Taxaceae was also abundant during the Mesozoic, both sub-families being represented. Some of the representative genera are: *Nageiopsis* of the Lower Cretaceous; *Palissya* of the Triassic and Jurassic; *Stachytaxus* of the late Triassic which had large cupuliferous seeds comparable with those of the modern *Dacrydium; Cephalotaxopsis*, *Protophyllocladus*, *Palaeotaxus*, *Tumion*, *Vesquia*, etc. The determinations of these forms rests not alone upon impressions of the foliage but upon seeds and cones and structural material of all classes, so there can be no

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question but that the Taxaceae were more differentiated and more abundant during the Mesozoic than at the present time, or that in those early days genera were cosmopolitan that have since become isolated, of which *Tumion* affords an excellent illustration.

Of the three subfamilies into which the Pinaceae are commonly segregated both the Taxiodieae and Cupressineae appear to precede the Abietineae in the geologic record and to be much more common during the Mesozoic. *Sequoia*, which survives in such grandeur in California, is represented continuously from the late Jurassic onward.

The Actinostrobinae, easily recognized, are represented by *Widdringtonia* and *Frenela* at a majority of the Mesozoic outcrops. The subfamily Abietineae as compared with the other two subfamilies is relatively modern. There can be no question of the evidence of the geologic record on this point, for while the Abietineae are well represented toward the close of the Mesozoic they are greatly outnumbered and completely overshadowed in differentiation by the Taxaceae and Araucariaceae and by the subfamilies Taxodieae and Cupressineae. The record is completely in accord with the older views that the Abietineae are the most specialized and most modern conifers, and although this relationship is questioned by Jeffrey, his theory of the origin of the Coniferales from a primitive Abietinean stock cannot be said to have convinced many students who have a first hand knowledge of paleobotany.

CENOZOIC HISTORY

The Cenozoic era was a time during which the floral types were essentially modern in character. Their most marked features were their arborescent richness as compared with existing conditions and the very general cosmopolitanism of the different types. The development of arid conditions over large areas in North America, Asia, Africa and South America, and the marked effect of the subsequent Pleistocene glaciation, were the main factors in the gradual segregation of these Cenozoic floras into more or less detached regions. No traces of Cycadeoidales or

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Williamsoniales are known from the Cenozoic and the Cycadales are seldom found. *Zamites* occurs in the Lower Eocene of Louisiana and in the Oligocene of France. The genus *Encephalartos* has been recorded from the late Oligocene of Greece, and *Dion* and *Cycadites* have been somewhat doubtfully determined from the Miocene of southern Europe.

The Ginkgoales are well represented during the earlier Tertiary. I have collected hundreds of beautiful fossil *Ginkgo* leaves from regions in western Montana now given over to Spruce and Cottonwood. Several undoubted species occur over an area that includes the Isle of Mull, Greenland, Sachalin, Siberia, Canada as far north as the mouth of the Mackenzie, Wyoming, Montana, etc. The later Tertiary records available do not contain *Ginkgo* except one or two instances from the Pacific coast of the United States and from southern Europe.

All three existing families of Coniferales were represented throughout the Cenozoic. The Araucariaceae show a progressive shrinking of range toward the south, although *Araucaria* is present in the Eocene of Europe and *Dammara* in Eurasia. The subfossil records show that the range of both of these genera is still shrinking at the present time.

Among the Taxaceae, *Podocarpus* is present in some force in the European Tertiary, *Cephalotaxus* foliage and fruits are present in both Europe and North America. *Taxus* and to a less extent *Tumion* are quite generally distributed. Among the Pinaceae, *Pinus*, *Glyptostrobus*, *Taxodium*, *Arthrotaxus* and *Cryptomeria* are quite generally distributed in the North Temperate Zone while the genus *Sequoia* is truly cosmopolitan.

Sequoia is found throughout both the northern and southern hemispheres and its wood showing perfectly characteristic structure demonstrates its presence in Europe until the dawn of Pleistocene glaciation. The accompanying sketch map (fig. 1) shows the Cenozoic occurrences of this interesting genus.

Taxodium and *Glyptostrobus* had an equally wide range in the northern hemisphere but appear to be absent in the southern. The genera *Frenela* and *Widdringtonia*, lumped with *Callitris* by Eichler, are not known from North America after the Mesozoic but they are common forms in the Cenozoic of Europe.

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RECENT HISTORY

The existing Coniferales are prevailingly temperate types and form vast forest areas especially in the north. They show a somewhat less southern massing, the two regions being separated by a broad tropical belt united only in the Andean and East Indian regions, but continuous in Tertiary times.

It is beyond the province of this paper to discuss the recent distribution of gymnosperms but it may be pointed out that this distribution is fully explained by the details of geologic history. The present occurrences of such genera as *Tumion*, *Libocedrus* and *Callitris* are readily understandable if their former distribution is taken into the account. The use of the terms endemic and monotypic becomes then singularly inappropriate when applied to genera like *Taxodium*, *Sequoia*, *Cunninghamia*, *Cryptomeria*, etc.

The accompanying diagram (fig. 2) furnishes a graphic summary of the foregoing discussion, illustrating not only the filiation of the principal types of gymnosperms, but also their relative abundance during the different eras.

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THE DAILY MOVEMENTS OF LEGUMINOUS LEAFLETS

FRANK C. GATES

Carthage College, Carthage, Ill.

Photeolic, nyctotropic, or sleep movements of certain leaves, particularly those of leguminous plants, are well known. The normal day position of the leaflets is in a plane nearly at right angles to the light. At night one of two distinct positions is assumed. In certain species this consists of a folding upwards and forwards, while in other species the leaflets droop or hang straight down. Members of the Mimosatae and Caesalpiniatae are examples of the first class and those of the Papilionatae of the drooping position. The movement is brought about by differential turgor in the pulvini of the leaflets in response to the stimulus of changing light and darkness in combination with higher and lower temperature. Just how this brings about the differential turgor is not at present understood.

In addition to the photeolic movements just noted, another movement takes place under certain conditions during the daytime. This I have termed the *xerofotic*[1] movement from the fact that it is due to differential turgidity in the pulvini caused by a greater drying effect on the upper side under one-aided illumination.

In nature this movement takes place under the influence of direct sunshine. In *Gliricidia sepium* it may be brought about by the local application of chemical drying agents, as absolute alcohol and xylol. The xerofotic movement in leguminous leaflets consists of an upward bend of the whole leaflet to an angle of between 45° and 70° above the horizontal. This position is maintained until the difference in turgidity is equalized. If of large size, clouds passing over the sun are sufficient to permit such equalization. Equalization always takes place as the sun

[1] Gates, F. C., Xerofotic Movements in Leaves. Bot. Gaz., 1916 (edition).

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begins to go down in the west. The xerofotic response is particularly noticeable during the hot or dry season, since the sun is much in evidence during that time. In a rapid assumption of the xerofotic position a certain amount of upward curling is noted at the tip of the leaflet. This upward curling is a form of the generalized type of xerofotic response in contradistinction to the localized type, in which the difference in turgidity is localized in the pulvinus.

In giving a daily program of the movements of leguminous leaflets, two classes must be considered according to the night position of the photeolic movement. In *Gliricidia sepium*, as an example of plants with a drooping night position, we have the following changes of position during the 24 hours. From the drooping night position of the leaflets we have the gradual change to the horizontal position as the sun rises. The beginning of the change generally takes place before the sun is actually above the horizon, but the completion is not effected prior to sunrise. On cloudy days this movement takes place somewhat later in the morning. Dark chamber experiments have shown that this change is a weak habit and will persist for a couple of days in the absence of the usual stimuli. On cold mornings—that is, with the temperature below 70° F.—the movement is noticeably delayed.

With the assumption of the horizontal position the leaf is in the "day" position. This should normally be maintained until a little before night. However, if the sun is shining strongly on the leaf, another movement will take place. This is the xerofotic movement. The cells of the upper side, exposed to the direct sun, lose more water and are consequently less turgid than those of the under, less exposed side. If for any reason, the direct sun is cut off from the leaf the horizontal position is resumed. If, however, the sun remains strong throughout the day, the xerofotic position is maintained until the effects of the sun are lessened by its sinking in the west. Thereupon the horizontal position is assumed and maintained until the conditions for the photeolic movement are brought about. In the group, of which *Gliricidia* is a member, this consists of a movement of the leaflet from the horizontal position to the drooping

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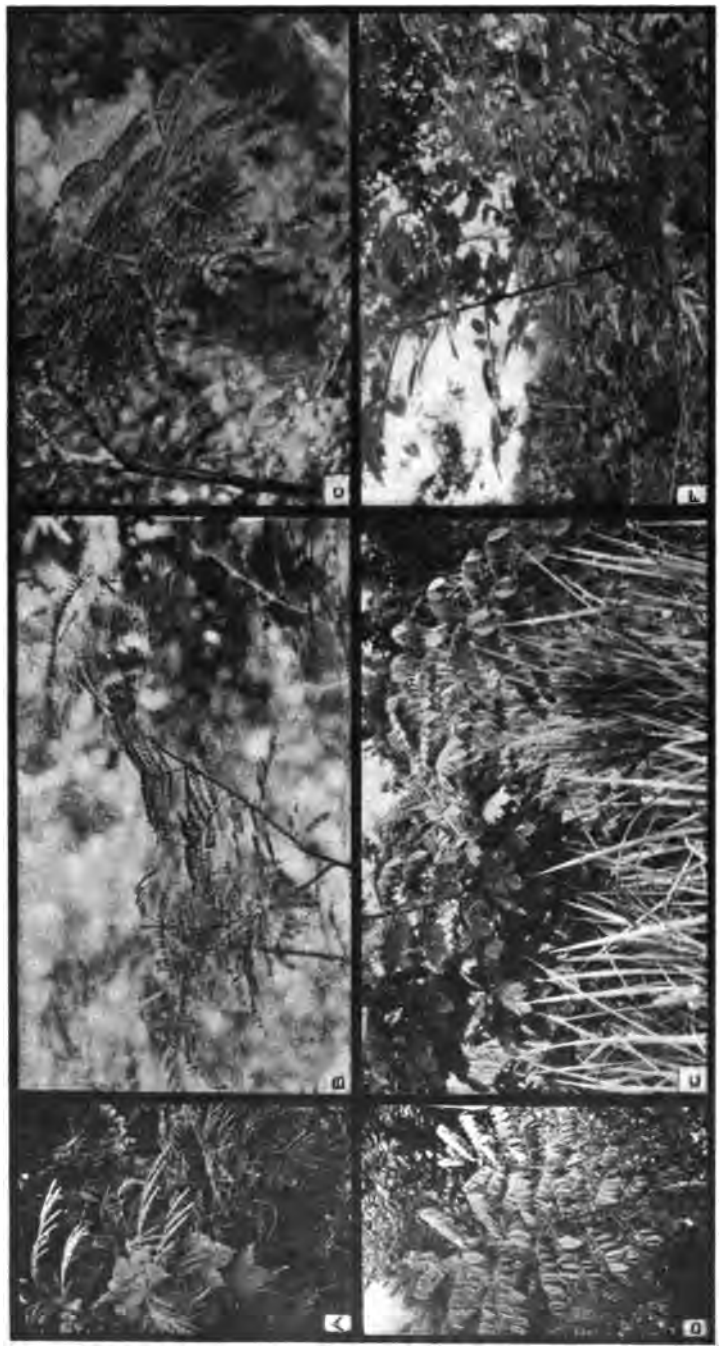

Fig. 1. A. *Leucaena glauca*, showing leaflets in the night position. Los Baños, P. I. June 20, 1913. B. *Leucaena glauca*, showing leaflets in the horizontal or normal day position. Los Baños, P. I. July 18, 1914. C. *Leucaena glauca*, showing the leaflets in the xerofotic position assumed under the stimulation of direct strong sunlight. Los Baños, P. I. July 29, 1914. D. *Gliricidia sepium*, showing leaflets in the night position. Los Baños, P. I. June 23, 1913. E. *Gliricidia sepium*, at sunrise, showing the leaflets midway between the night and the day positions. Los Baños, P. I. June 20, 1913. F. *Gliricidia sepium*, showing the leaflets in the horizontal or day position. Los Baños, P. I. June 21, 1913.

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position, a fall of 90°. This change—like the others—can be seen with close observation. It is completed in about 20 minutes. At the close of the movement the leaflets are down, lower side to lower side. This position is maintained during the night. It may be somewhat disturbed at the time of full moon.

In *Leucaena glauca*, we have an example of a group of plants in which the night position is above the horizontal instead of below it. The leaflets fold forwards as well as upwards and overlap. At break of day the leaflets begin to bend back. The tip of the leaflet is the first part to show response. Gradually the whole leaflet bends out and back until it reaches the hori-

Fig. 2. A. *Gliricidia sepium*, showing the leaflets in the xerofotic position in strong sunlight. Los Baños, P. I. June 24, 1913. B. *Canavalia lineata*, showing leaflets in the xerofotic position. Taal Volcano, P. I. March 7, 1915.

zontal or day position. As in the other group, this position is maintained until dusk, unless affected by strong, direct sunlight. In this case the xerofotic response is brought about. In every way the xerofotic position of this group is similar to the other, as described in *Gliricidia*. The same factors govern resumption of the horizontal position under suitable conditions during the day and at dusk. At dusk, however, the movements are upwards and forwards into the night position. The night position is maintained during the night, subject to the same irregularity at the time of full moon, but in this respect *Leucaena* is less affected than *Gliricidia*.

The figures bring out the different positions.

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PARCH BLIGHT ON DOUGLAS FIR IN THE PACIFIC NORTHWEST

THORNTON T. MUNGER

Forest Service, Portland, Oregon

Quite frequently in the spring of the year the foliage of the Douglas fir trees in the vicinity of Portland, Oregon, turns brown. In March and April entire trees are sometimes as sere as though they had died recently, and groves look from a distance as though a hot fire had scorched them. The injury is sometimes so striking as to give rise to the impression that all the timber is dying. But with the beginning of the growing season most of the buds open normally and by midsummer the trees have regained their usual green appearance. Close examination in midsummer indicates that many of the old needles are brown and are dropping off, and that in places the one-year-old twigs have been killed.

The injury is most serious on isolated, exposed trees, on the eastern sides of these trees, and on the eastern edges of groves. Trees on the western side of dense groves show almost no signs of the injury. Trees of all ages apparently are equally affected. It is also noticeable that timber on exposed hillsides facing the east is more subject to injury than that in protected locations. Some of the species associated with Douglas fir are also browned, but to a less degree.

For several springs there has been some evidence of "the blight" in the vicinity of Portland, but it was particularly noticeable in 1913 and 1915.

The cause for the blight is rather easy of explanation, but none the less interesting to the plant physiologist and to the forester. It is due to the drying east winds—the Chinook winds—that occasionally sweep across the Cascade Mountains from the interior plateau country and parch the Douglas firs,

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which are used to the humid insular climate of the region west of the Cascades, at a time of year when their physiological functions are least active and they are least able to withstand this parching. It is apparent that the injury is more severe in the vicinity of Portland because this region is particularly exposed to the direct sweep of the east winds down the canyon of the Columbia River. The injury has, however, been reported from a number of other points in Western Oregon and Washington, where the dry winds from the interior have evidently been active.

The Douglas fir of the region west of the Cascades is called the Coast form, and it is particularly dependent upon a humid mild climate. The Douglas fir east of the Cascades in Oregon resembles the Rocky Mountain form, and it endures a much drier and severer climate. It is interesting, therefore, to note that in passing up the Columbia River evidences of the injury disappear at about 35 miles eastward from Portland at a point about opposite the crest of the Cascades, where the Douglas fir takes on the hardier characteristics of the Rocky Mountain form.

Usually the affected trees show no permanent ill effects from this parching, though undoubtedly the loss of part of their foliage inhibits their growth. In particularly exposed spots, such as at Crown Point on the Columbia Highway, the old trees have very narrow spire-shaped crowns, due, no doubt, to the annual parching of their tender twigs by these dry winds. Often their foliage is largely on the western side, but yet the crown has not the shape of the typical wind-swept seaside tree.

This form of injury is analogous to the "Winter Injury of the White Pine in 1908" in Maine, described by Mr. W. J. Morse in Bulletin 164 of the Maine Agricultural Experiment Station. It also has much in common with the so-called (and I might add unfortunately named) "red-belt disease," which is a not infrequent climatic blight of the timber fronting on the desert in an arid country.[1] I suggest "parch blight" as an expressive and distinguishing name for this injury.

[1]Hedgecock, G. G., Winter-killing and smelter-injury in the forests of Montana. Torreya, vol. 12, no. 2.

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BOOKS AND CURRENT LITERATURE

WESTERN ALGAE.—There recently appeared the earlier numbers of the Publications of the Puget Sound Marine Station, issued under the editorship of Prof. T. C. Frye, of the University of Washington, Director of the Puget Sound Station, which is located at Friday Harbor, Washington.

It is fitting that the series should be opened with records of observations and experiments with the big kelps[1] of the locality—plants of double interest now that they are recognized as a potential source of potash on a commercial scale. The first paper deals with the rate of the growth of the fronds or leaves of this striking plant. Preliminary experiments soon showed that *Nereocystis* would grow as well when loosened from the natural foothold on the rocks, provided the plants were not carried into unfavorable conditions. Entire plants, and plants with stalks wholly or partly removed, were anchored in various relations in the water and "grew apparently as well as firmly anchored plants." The holdfast serves only to fix the plant in place. The laminae of these plants during the first week of July grew quite rapidly, varying with the stage of development from one eighth of an inch to two and one-fourth inches daily. A second set of experiments, with fronds cut at varying lengths from the bulb, showed an increase in amount of growth with length of frond, thus indicating that the region of growth was not sharply localized. Subsequently it was established that there is little growth in the laminae beyond 2 feet from the bulb, and that the region of maximum elongation is the zone between 3 and 6 inches from the float. During the course of these observations it was determined that small fragments of the thallus cut out from the leaves would live and grow for some time. Pieces, some measuring only ½ inch by ¼ inch, exhibited growth for a period of seven days, at the end of which time the reviewer infers the parts were still living. It was noted that the kelps grew more rapidly on some days than on others. According to records in 1914 the greatest growth was on those days with most wind; since the experiments were conducted in a region

[1] Fallis, Annie L., Growth of the fronds of *Nereocystis luetkeana*. Pub. Puget Sd. Marine Sta. 1: 1–8. January, 1915.

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of fairly even sunshine and the water temperatures were not liable to great fluctuation the inference seems safe that the more rapid growth on windy days was probably due to the better aeration of the water when disturbed by air currents.

A second paper[2] dealing with this big kelp takes up the rate of growth of stipe of *Nereocystis*. Some difficulty was experienced in finding a satisfactory method of measurement. The plan finally adopted after preliminary study was to take healthy plants freshly pulled from their natural anchorage and to attach these to the lower portion of a raft which in turn was moored in the margin of a vigorous kelp bed. A fortunate control was found in plants, which, on being pulled from their original place of growth, brought their anchorage rocks up with them. These could then be returned to normal conditions each time after measurement thus giving a control on the other measurements. The two sets of plants were found to agree in their rate of growth. Fourteen plants under observation for periods varying from two to twenty days displayed a rate of growth in the stipe ranging from ¼ inch to 2½ inches per day—averaging about 1 inch per day. An old plant which had survived the previous winter had a stipe over 47 feet in length and showed no further growth. Further study showed that the region of elongation in the stipe is not so sharply localized as in the fronds but involves the whole region from bulb to holdfast. The region of greatest growth, however, is the lower hollow portion of the stipe, which lengthens much faster than either end of the stem. Cut stipes usually die, apparently from the action of organisms at the cut surface or in the interior of the central cavity.

Another paper[3] of the series outlines the results of a set of experiments to determine the ability of sea weeds to withstand desiccation. These studies continued for a month, and the proof of death from desiccation was the inability of the plant to resume growth when brought again to favorable relation on the shore. Thirteen species were studied, ranging in habitat from high on the rocks to well toward the low tide line. The results showed that the ability of the these algae to withstand desiccation agrees with their relative position above the low tide mark and consequent period of exposure between tides. The experiments were conducted upon one green alga, five brown algae, and seven red algae. *Fucus evanescens*, *Gloiopeltis furcata*, and *Gigartina*

[2] Sheldon, Sarah M., Notes on the growth of the stipe of *Nereocystis luetkeana*. Pub. Puget Sd. Marine Sta. **1**: 15–18. January, 1915.

[3] Muenschner, Walter L. C., Ability of sea weeds to withstand desiccation. Pub. Puget Sd. Marine Sta. **1**: 19–23. February, 1915.

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mamillosa were found able to resume growth after an exposure of forty-eight hours, while plants living lower on the shore were unable to withstand a single hour of exposure. *Desmarestia aculeata*, *Alaria valada*, and *Sarcophyllis californica* were representatives of this latter group. Intermediate forms, occurring midway on the rocks, will withstand two hours of continuous desiccation; among these are *Rhodomela larix* and *Colpomenia sinuosa*. While it is not claimed by the writer that the ability to withstand desiccation is the only reason why some algae grow high on the rocks and others are limited to the regions near the low tide line the data show conclusively that drought is one of the reasons why some forms at least can not grow in places where they will be subjected to long exposure.

The description of a new species[4] of green alga from the region of the Puget Sound Station is recorded in another number of the publications. Frye and Zeller describe the form as differing from the other species of the genus in the possession of gametes having four cilia instead of two as in forms previously studied. This modifies our conception of the genus. The new form, *Hormiscia tetraciliata*, is nearest to *H. collabens* (Ag.) Rabenh. and *H. incrassata* (Kjellm.) Collins, but has larger cells than either of these. It has been referred to *H. wormskjoldii* (Mert.) Fries, but differs from that species in having much narrower filaments. The plant was found at several places in the vicinity of the Puget Sound Station.—R. B. Wylie.

Osmotic Pressure in Saprophytes and Parasites.—G. Senn[5] determined the concentration of the sap of a number of plants from Java cultivated in locality and conditions not described, and found that thick-leaved epiphytes were not higher in turgidity than terrestrial species of the same region, while the sap of thin-leaved species was distinctly more concentrated. An estimation of the relative concentration of such parasites as *Viscum*, *Orobanche*, and *Pedicularis* and their hosts gave a higher concentration of sap in the parasites of 0.025 to 0.625 Mol. $K\ NO_3$, the lower figure being equivalent to less than 3.5 atmospheres. The relative concentration of sap of host and parasite has received some attention experimentally, but the author comfortably confines himself to a citation of the articles published in Jena.—D. T. MacDougal.

[4] Frye, T. C., and Zeller, S. M., *Hormiscia tetraciliata* sp. now. Pub. Puget Sd. Marine Sta. **1**: 9–13. January, 1915.

[5] G. Senn, Der osmotische Druck einiger Epiphyten und Parasiten. Verh. d. Naturforsch. Gesell, v. Basel. **24**: 179–183, 1913.

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NOTES AND COMMENT

A meeting of ecologists was held at Hotel Hartman, Columbus, Ohio, on December 28, 1915, under the chairmanship of Prof. J. W. Harshberger, for the purpose of considering the organization of an ecological society. About fifty persons were present, nearly all of whom were enthusiastically in favor of forming such a society. Over fifty others who could not be present had notified the Secretary of their interest in the movement. In view of these facts it was definitely voted to organize under the name The Ecological Society of America. It was decided to regard as charter members not only those present at the organization, but also those who had by letter expressed a desire to be included in the membership, as well as those desirous of joining prior to April 1, 1916. The new society thereby has an initial membership of more than one hundred botanists and zoologists interested in ecology. The following constitution was proposed by the organization committee and adopted.

CONSTITUTION

ARTICLE 1. The name of this Society shall be The Ecological Society of America.

ARTICLE 2. The object of this Society shall be the promotion of the interests of ecology.

ARTICLE 3. *Membership.* Membership in this Society shall consist of persons interested in ecology. Names of candidates for membership may be submitted by any two members to the Secretary-Treasurer, and presented for election at the next annual meeting

ARTICLE 4. *Officers.* The officers of this Society shall be a President, Vice-President, and Secretary-Treasurer. These officers shall constitute the Executive Committee of the Society, and shall be elected by the Society at the annual meeting, from nominations made by a committee of three appointed by the chair, or from nominations from the floor.

ARTICLE 5. *Meetings* There shall be a stated annual meeting held in accordance with the action of the Society at the preceding annual meeting, and such field meetings as shall be initiated by any group of members. The Secretary-Treasurer shall give full advertisement of all such field meetings.

ARTICLE 6. *Dues.* The annual dues of the Society shall be $1.00.

The officers chosen at the organization meeting were: President, Prof. V. E. Shelford, of the University of Illinois; Vice-President,

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Prof. W. M. Wheeler, of Harvard University; Secretary-Treasurer, Dr. Forrest Shreve, of the Desert Laboratory. The first regular annual meeting will be held in New York during the next Convocation week, where a program will be worked out in harmony with the programs of the botanists and zoologists so as to minimize serious conflict. A field meeting will probably be held in Chicago in June.

The Bulletin of the American Geographical Society has been discontinued after a career of sixty-three years, its place being taken by *The Geographical Review*, a journal of slightly greater size but of similar contents. This change is made as one that befits the widening scope of the organ of the Society and as a testimonial of the intention of the Director, Dr. Isaiah Bowman, to still further improve upon the standard of interest and usefulness which was maintained by the Bulletin for so many years.

Among the papers which will appear in forthcoming issues of THE PLANT WORLD may be mentioned: The Red Color of the Mesocarp of Seeded Fruits in the Persimmon, by Francis E. Lloyd; The Weight of Physical Factors in the Study of Plant Distribution, by Forrest Shreve; Notes on the Ancestry of the Beech, by Edward W. Berry; A Critique of the Hypothesis of the Lime-Magnesia Ratio, by Charles B. Lipman; A Study of the Relation of Soil Moisture to Transpiration and Photosynthesis in the Corn Plant, by T. G. Yuncker; and The Forests of the Hawaiian Islands, by Vaughan MacCaughey.

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THE WEIGHT OF PHYSICAL FACTORS IN THE STUDY OF PLANT DISTRIBUTION[1]

FORREST SHREVE

The Desert Laboratory, Tucson, Arizona

We have in our possession a truly prodigious and rapidly growing body of facts relative to the distribution of terrestrial flowering plants. These facts have been recorded, arranged, and classified by students of plant geography, and many men have yielded to the essential scientific impulse of attempting to explain them. The task of explaining the distribution of plants is one of such immensity, such complexity, and of such wide dependence on related sciences that its progress is a prolonged and slow one, working through a multitudinous array of facts toward the ultimate goal of general principles.

The search for underlying causes in plant geography may concern itself with the total ranges of plants or with the local or habitual occurrence of these plants within their areas. The student of general distribution has been concerned with the delimitation of floral regions and the evolutionary history of their species, and has invoked his aid chiefly from paleobotany. The student of local distribution has been concerned with physiological or ecological aspect of the subject, and has called to his aid all of the physical sciences.

So sharply drawn has been the line between the study of distribution as a floristic subject and its study as an ecological subject that we have been prone to lose sight of the commanding and obvious features which are common to these adjacent lines of work.

The surface of the earth presents a large number of dissimilar climates, merging into one another, and an enormous number

[1] Paper read in the symposium on Geographical Distribution at the meeting of the Botanical Society of America at the University of California, August 5, 1915.

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of habitats, differing by greater or less degrees. The major task of plant geography is to determine the causal relation of these environic conditions and sets of conditions to the manifold facts of distribution. Each successive geological epoch has presented problems of the same kind that are presentd by the distribution of plants today. We can scarcely hope to learn more than the merest outlines regarding the ancient distributions of plant stocks, and the history of the genera which are still represented in our floras. We can, however, learn much in regard to the influences at work at the present time in determining the general and the habital distribution of plants.

It is our custom to speak of the "historical factors" and the present factors operative in determining plant distribution. We must bear in mind that when we speak of historical factors we are embracing in the term two very dissimilar things which have registered a combined effect. We must look to evolutionary history and to paleobotany to tell us where, for example, the genus *Sequoia* originated, at what epoch, and from what stock. We must look to paleobotany and paleoclimatology to tell us what have been the movements, the extensions and retreats of *Sequoia*. The initiation of a species is—from our standpoint—purely an evolutionary event; the history and fate of a species after its initiation are decided by the changes in orography or climate which it encounters, with the possible participation of physiological changes in the stock of such nature as to be unaccompanied by morphological modifications of diagnostic value. It is conducive to clearer thinking, therefore, to distinguish between the evolutionary factors and the paleoclimatic factors which compose the historical factor. This distinction has its principal value in compelling us to regard the present distributional phenomena of the earth as merely a moment in the prolonged and incessantly active procession of change due to secular or sudden changes of climate, or to destructive or constructive events in surface geology, and discontinuously marked by evolutionary activity. We are able to realise that there is no gulf between the climate of the past and that of the present; and that there has been no sudden, extensive or unaccountable readjustment of distributions.

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The evolutionary factor in distribution presents its own problems, but they are so difficult and at present so far from any hopeful prospect of solution that we must be content to let them alone. Who is there among us who is willing to state why the Cactaceae originated in America and not in Africa, when we are not even certain as to the nearest living relatives of this family? Who will state why the graminean stock has become so widely disseminated and has colonised such dissimilar habitats and climates without exhibiting a greater morphological differentiation?

The rôle of the evolutionary factor can not be escaped in any consideration of distribution. We owe it to the history of the great plant stocks that *Yucca arborescens* occurs in the Mojave Desert and that *Aloe dichotoma*, somewhat similar to it in form, grows in the deserts of South-west Africa. It is likewise a part of phylogenetic history that very many plants were formerly confined to particular regions whereas they have now been introduced over seas into climates which prove to be wholly congenial to them. However, the ranges of *Yucca* and *Aloe* in their respective continents are to be sought in the operation of the environment, and the spread of an introduced plant in a new continent is controlled by physical factors just as it was in its native continent.

Evolutionary activities and phylogenetic history are to be thought of as supplying the raw materials out of which the physical environment has made the present distributional complex of the earth's surface. We can not hope at present to understand why we have a strong development of the genus *Yucca* in the southwestern United States and a rich development of *Aloe* in South Africa, and the answer to such a question, if forthcoming, would have only a remote relation to the study of the present influences which are limiting the distribution of the members of these two stocks in their respective contients.

The rôle of the paleoclimatic factors is also an immanent one in the determination of plant distribution. Many species have a known ancestry and a known ancestral range, at the same time that they now inhabit areas of such small size that it is

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difficult to believe that any present physical factors are restricting them. The history of these plants has been one of extinction and retraction, due to changes in their old extended environment. They are now unable to regain their old ranges, or even to spread over relatively short distances. These species may well be looked upon as physiologically and genetically decadent. They are probably limited in distribution because they have failed to change their requirements to that slight extent which might permit a greater extension under altered conditions, and they are old simply because they have failed to change to that greater extent that would have reacted upon form in such a manner as to make us regard the resulting plants as a distinct species from the old ones.

In addition to the old and restricted, or relict, species we have another class of plants of limited range, those which are apparently just appearing on the scene and have not yet had time to occupy the entire area in which they might be expected to find congenial conditions. These plants are generally members of large genera such as Opuntia, Antennaria and Crataegus, or else of genera which have been recently subdivided, whereas the relict species are usually members of small genera. It is not always easy to decide whether a given restricted distribution is of the relict type or of the "novitiate" type, as we may call the emerging species. Our decision—in the lack of other evidence—is apt to be based upon the existence or absence of fossil records of the species or its allies, or else upon the size and phylogenetic position of the genus or family. Such a restricted conifer as *Pinus mayriana* may well belong in either class, and the members of many small or monotypic genera of Mexican Compositae may also stand in a doubtful position.

A very considerable number of our plants belong neither to the relict nor to the novitiate class. They are of such age that they have had time to extent themselves as far as the subtle factors of their environment, the crude power of great barriers, or the operation of suitable agents of dispersal have permitted them, and their course has not run so far that climatic and orographic calamities have overtaken and restricted them.

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This great class of physically controlled plants can not be specifically enumerated at the present time. There are many good reasons for believing it to contain the bulk of the species which form the dominant element in all vegetation, whether these are plants of extended range and frequent occurrence, plants of more restricted range, or plants whose occurrence is determined by constellations of conditions which are themselves rare. We may find areas of vegetation in which a relict plant is dominant, as is true of the groves of *Cupressus macrocarpa* near Monterey, California, or others in which a novitiate plant is very abundant, as is true of the Cababi Hills, in southern Arizona, where an undescribed *Opuntia*, known nowhere else, is extremely abundant. Although cases of this sort are fairly common they are usually readily detected by a more thorough study of the adjacent regions. Such trees as *Liriodendron*, *Taxodium*, and *Liquidambar* are known to have undergone distributional recessions, but they occupy such large areas at present that they can scarcely be classed as relict species, and can surely be placed among the plants whose distributional controls are worth looking for among factors at present operative. Whether the physically controlled plants form a large or a small percentage of our flora we can at least state with some assurance, based upon the correlation of distribution and climatic conditions, that they form the predominant part of our vegetation. The great bulk of the trees, shrubs, grasses, root-perennials and other plants which make up the dominant natural vegetation of the world may safely be held to have had their present distributional limits imposed by physical factors which are either now operative or were operative in very recent time. Such factors may be acting directly through the conditions of climate and soil, or may be acting indirectly through geographic or physiographic changes, through the influence of associated plants, through animal, fungal or bacterial enemies, through fire or mechanical agencies, or through the means of animate or inanimate agents of dispersal. Since these indirect factors of environment can affect plants only through the same kinds of physiological influences as are exerted by the direct factors of the climate and soil they are at bottom

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of the same nature whether we allude to them as "biotic" factors, "mechanical factors" or what not. These two classes of factors are further distinguishable in the fact that the direct ones are chiefly constant in their operation, while the indirect ones are intermittent or discontinuous in all cases.

In the isolated desert mountains of southern Arizona the great bulk of the species are physically controlled in their distribution, as is abundantly shown by the universality of each of these species throughout a given altitudinal range or a given set of habitats, and by the definiteness with which it is limited by rather sharply drawn lines. When one of these mountains is compared with another the flora is found to be closely similar but not identical. Certain species range over the western Cordillera of Mexico or over the central Rocky Mountains and have reached certain of the isolated desert mountains without having reached all of them. At least a few cases are known in which a given species is common throughout several mountains and is known from only one or two restricted localities in another mountain, although an immediately contiguous area of favorable environment awaits it. In view of the universality of the distribution of most of the mountain flora these cases appear to be the opening invasions by which new components are being added to the flora. They are in a way analagous to the novitiate species of larger areas, and their presence in no way vitiates the evidence for the physical control of the distribution of the major portion of the mountain flora.

Wherever I have had an opportunity to study vegetation with any knowledge of the physical conditions attending it, there has been patent evidence of the control which these conditions exerted over the local and general distribution of the common components of the vegetation. This control is more sharply manifest in the desert mountains of southern Arizona than in other localities which I have seen, because of the great differences of climate encountered within short vertical distances. The force of the physical controls is almost equally patent, however, along the greatest east and west diameter of Texas, where the changes of elevation are small and differences of soil

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accompany those of climate. It is obvious in Maryland and the adjacent states, where the texture and mineralogical origin of the soils is the dominant controlling group of factors. It is also obvious in Jamaica, where, for the island as a whole, the vegetation is controlled by an intricate interaction of temperature, moisture and soil conditions.

It is clear that we can not formulate the principles which are involved in the causation of plant distribution without a consideration of the relict and novitiate species as well as those that are physically controlled. We can not, however, invest gate these three types of distribution by the same methods. The paleobotanist must help us to elucidate the relict distributions and the geneticist must help us to recognise and explain the novitiate ones. It is the physically controlled distributions of which I wish to speak further.

For over twenty years we have witnessed the active studying of vegetation, a line of work which has been fruitful from our standpoint because it has given small attention to floristics and has laid emphasis on the relation of plants to their environment. This work has been devoted mainly to the study of plant communities of various ranks, the description of their physiognomy and component species, the investigation of their relationships and movements, and the determination of the causes underlying these movements. The communities have been studied as entities in themselves, they have been looked upon as having a definite type of communal behavior, and have even been likened to individual organisms.

The study of vegetation has been chifly concerned with the habital distribution of plants, and has not been consciously directed toward a solution of the problems of general distribution, although the ultimate questions raised in vegetistic work have been those which are fundamental to all aspects of distributional investigation.

The collective or communal behavior of an assemblage of plants is determined by the physiological behavior of each of the species present in the assemblage. The distributional limitation of all physically controlled species is also determined by

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their physiological behavior in relation to environment. It is for this reason that the ultimate questions of general distribution and those of habital distribution are so nearly the same. It is for this reason also that the study of distribution in the old sense of Grisebach and Hemsley and the study of vegetation in the sense of the present school of ecologists have so much common ground. We have been accustomed to feel that the evolutionary and paleoclimatic factors have so much to do with general distribution, and that such a strong rôle is played by agencies of dispersal, biotic factors, mechanical agencies and the like, that the impossibility of completing our knowledge of the operation of these factors, or the impossibility of experimentation in regard to them, made it advisable to pass the subject on to posterity for solution. We have turned to the study of vegetation and the distribution of physically controlled plants as presenting more tangible and more solvable problems.

The natural communities of plants, considered either in a large or in a small sense, vary greatly in the number of species which they contain. Some of them present the extreme simplicity of a pure stand, as the marshes of *Spartina polystachya* on the Atlantic coast, many others are relatively simple, still others are rather rich, and a great many are highly complex, containing a large number of very dissimilar species, as is true of the fresh-water marshes of the Atlantic coast, of such tropical rain-forests as have been described by Warming and by Spruce, and of the deserts of Arizona and the South African Karroo. In all of these communities, even those which are rich in species, we have a certain degree of similarity in the physiological requirements of the species which are dominant, that is to say, of the species which are most directly influenced by the climatic conditions. It is only, however, by speaking in the very broadest terms that we can allude to these associated plants as being similar in their life requirements. In a more exact analysis of the relation of these plants to their physical surroundings we find them highly unlike. In fact we have no warrant for supposing that two plants which grow side by side and attain the same height are subjected to the same constellation of conditions. I may men-

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tion in this connection some of the features of the Encinal, or evergreen oak region, of the mountains of southern Arizona. This assemblage is made up characteristically and uniformly by such dissimilar forms as the evergreen broad-leaved oaks, the evergreen needle-leaved piñon, the evergreen scale-leaved juniper, several evergreen broad-leaved shrubs (*Arctostaphylos, and Garrya*), the stem-succulent grass-like *Nolina* and *Dasylirion*, the leaf-succulent *Agave*, the stem-succulent *Opuntia*, the small deciduous and fine-leaved *Acacia* and Mimosa, the large-leaved and deciduous *Ingenhousia* and *Erythrina* the small and hoary-leaved species of *Artemisia* and *Eriogonum*, and a multitude of equally dissimilar shrublets and root-perennials. These plants live together under the conditions which prevail between 4500 and 5500 feet of elevation. The dissimilarity of general physiological behavior and collective life requirements which is indicated by the unlike features of form in these plants is confirmed by their unlike general distributional ranges, by the fact that some of them range lower toward the desert than others, while some ascent to the forested elevations. Their dissimilarity is further attested by what we know of the root habits, growth phenomena and seasonal behavior of the members of the community. Unpublished work which I have recently carried out with relation to the transpirational behavior of this assemblage of plants still further and still more concretely emphasises the unlikeness of these plants which live in dissimilar relations to the environment, and even present habits of root distribution and of foliar periodicity that place adjacent plants under as unlike conditions as if they lived many hundreds of miles apart.

A very similar and almost equally striking condition exists in the desert valleys of southern Arizona, where a highly dissimilar set of species are found, almost any two of which may sometimes be found in close association, no two of which are invariable associates. These facts which are true of the southwestern desert region are also true, although less conspicuously so, in the moister portions of the United States. In the rainforests of Jamaica, both in the Blue Mountains and in the lower limestone hills, the diversity of life forms is almost as striking

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as in the deserts of Arizona, and the delimitation of plant communities with a reasonably constant composition is even more difficult than in the desert. In the forest and grassland areas of temperate climates the natural communities of plants are more simple in their composition and more distinctive in comparison with adjacent communities. From the standpoint of successional ecology every plant community, wherever found, constitutes a unit,—a definite entity. From the standpoint which I am desirous of taking, each of these communities is a collection of species with some very general resemblances and some very pronounced dissimilarities in their physiological characteristics. The findings of successional ecology will not aid us in learning the nature or intensity of the controls which limit a species to a particular geographical range or to a particular class of habitats.

In order to face squarely the problems of causation in both general and local plant distribution it is necessary to consider plants as physiological entities and not as phylogenetic entities. It is also necessary to give our most serious consideration to individual plant species rather than to plant communities. Our understanding of the limitation of general distribution, and of habital distribution as well, is dependent upon a fuller knowledge of the behavior of each of the physiological entities separately considered. Our physiological knowledge, which is so strong with respect to wheat and corn, *Vicia faba* and *Lupinus albus*, must be extended to a greater familiarity with the dominant plants of our leading vegetations, to a comparative knowledge of the behavior of plants which grow together in the same communities, and to a determination of the limiting factors which control the individual or collective physiological functions of the plant.

There are two important phases in the present physiological trend of work in plant geography and ecology. One is the establishment of correlations between the distribution of physical factors and the distribution, general or local, of plant species and communities. The other is the intensive study of a particular function, or group of functions, in a series of species which

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have some structural or habital relationship. These two phases of work constitute the more general and the more specific modes of attack upon the fundamental questions of the relation between the plant and its environment.

The number of workers who have carried out intensive observation of vegetational distribution and have correlated this work with instrumental measurement of factors is now quite large, and I need only mention a few such investigations as those of Hesselman in Sweden, of Shantz in the Great Plains, of Transeau at Cold Spring Harbor, of Rübel in the Alps, of Fuller in the Chicago region, of Weaver in Washington, and of Kraus in Germany.

We need a large body of such correlational work, both for its own sake and for the suggestions that it brings for the more specific or experimental phase of work. Although based upon the correlation of *vegetation* and physical environment, such work as I have mentioned serves to throw much light upon the general requirements of individual species, and is at least the stepping stone to the more exact knowledge of cause and effect, to which correlations can point but can not lead the way.

The amount of work on the comparative physiology of associated plants, or of plants of the same life form, is not so large. The work of Cannon on the distribution and optimum growth temperature of roots is of importance and of notable ecological interest. The work of Livingston and of Bakke on the comparative transpiring power of plants is calculated to lead the way to a precise knowledge of the transpirational behavior of associated and unassociated plants. The partially published work of Harris on the osmotic strength of the saps of plants from the same habitat, from different habitats and from widely divergent regions is a very fundamental contribution to causational plant geography. An important advance in our knowledge of comparative physiology has been made in the work of Richards, of MacDougal, and of Mrs. Shreve on several physiological aspects of the cacti. Their work, which I can not detail here, shows in how far these plants depart from the known physiological behavior of non-succulent plants, and has emphasised the possi-

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bility that further physiological exploration may discover in other plants equally great departures from the classic types of respiration, transpiration and water intake.

This is by no means the first time that an intensive physiological study of individual species has been urged as the only direct and certain road to a better understanding of plant distribution. The fact has been appreciated by many ecologists and physiologists and has been particularly emphasised by Ganong. Our interest in the individual species had its commencement, as have so many things in plant geography, with the observations of Humboldt on the rôle which different types of plants play in determining the physiognomy of the vegetation. Beginning with Humboldt's life-forms we have had many schemes for the rough classification of plants according to their size, form and gross anatomy. These schemes, propounded by Grisebach, Warming, Reiter, Raunkiär, and Drude, constitute a series of attempts to group plants according to their gross anatomical and physiological characteristics. Among these classifications of growth forms, life forms, or vegetation types, as they have been variously called, the more recent sympodial ones are a decided improvement over the older simple ones, and that of Drude, set forth in his recent Oekologie der Pflanzen is by far the best of them. These systems are of interest to us because they represent the crude beginnings of an attempt to construct a physiological classification of plants. The recent growth of interest in the system of Raunkiär in particular is a wholesome sign that we are beginning to take a closer look at vegetation and that we are gradually getting near enough to it to discern the individual species of which it is composed. I do not mean to commend the system of Raunkiär, which is too simple to fit the d versities of the vegetable kingdom, even crudely as we know them at present, and is based too largely on the single feature of the location and size of the perrenating organs of plants. Neither do I mean to commend the "biological spectra" of Raunkiär, which are of floristic interest but are rarely constructed from such data as to give them vegetistic value.

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What we have in such a system as the growth-forms of Drude is a confessedly rough but eminently natural grouping of plants according to their size and form, their manner of branching, the character of their foliage, the seasonal behavior of their foliage, and other features which stand in intimate relation to their gross physiological behavior. Some of the criteria used in separating the growth-forms appear to have only a morphological value, as that which places the palms in a separate category from other broad-leaved evergreens; many other criteria seem to lay special emphasis on the water relations, as those that have to do with succulence and the aphyllous condition. We are not in a position at present to know how much physiological significance there may be in the differences between the monocotyledonous stems of palms and the dicotyledonous wood of other broad-leaved evergreens. Neither are we in a position to appreciate how much the features of succulence and aphylly may affect functions other than those of water-loss, although the work of Richards to which I have referred gives some suggestion of the relation of succulence to respiration. In the main the criteria upon which Drude has based his system are of undoubted physiological value, and many of them are of such a nature as to be related to more than one set of major functions.

In brief, the system of growth forms of Drude is a rough attempt, on the basis of observational data, to classify plants according to their ecological characteristics. This is merely another way of saying that it and the other systems are the first expression of our need for a thoroughgoing physiological classification of plants. It is needless to say that such a grouping of plants must be based on experimental work, and that it must have no bias regarding the greater importance of water relations, of temperature conditions, of root distribution, of respiratory features, or of photosynthetic behavior. To be faithful to the facts, and to be useful as a tool—which is the chief value of any classification—this one must be a well balanced attempt to arrange plants according to a natural anatomical and physiological system, even in the absence of anything akin to phylogenetic relationship to serve as a guide.

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Students of vegetation are using at present a natural system of classification of types of vegetation, distinguishing evergreen and deciduous forest, grassland and savanna, heath and moor. Back of the patent dissimilarity of these communities lies the unlikeness of their dominant plants, and behind this unlikeness lie the anatomical-physiological differences between these plants. To learn more about the physiology of individual dominant species in the evergreen forest, the grassland or the heath will give us a more precise knowledge of the life-forms to which they belong, and will aid us in the investigation of the factors which limit the physically controlled species of these communities. A better understanding of the life-forms will give us a sounder basis for the distinguishing of types of vegetation. There is no importance in asking whether the nearly pure stands of *Covillea* which occur from the Mojave Desert to Zacatecas are desert, bush-steppe or chaparral. We should have for them something more than a casual examination, a personal opinion, and a colloquial or polysyllabic name. We can have it only by learning more about the physiology of *Covillea*. Such knowledge might elucidate the known distributional facts about some other similar shrubs, or it might emphasise the importance of studying the other shrubs as well.

The whole group of problems in the general and local distribution of physically controlled plants resolves itself into a painstaking study of the physiology of the plants and the physics and chemistry of the environment. We do not need the methods of physics and chemistry, as is so often said. We need training in physics and chemistry and we need methods of our own.

The subject of plant geography, considered in its widest sense, presents a field of enormous width, takings its facts from taxonomy, learning as much of the past as it can from paleobotany, using the methods and demanding the knowledge of the climatologist, the geologist, the physiographer, and the soil physicist, and carrying its ultimate problems to the physiological laboratory or to the specially equipped field station. The attack upon this wide field is at present being made upon its extreme edges. Those who form the attacking force are either advancing in the geo-

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graphical ranks toward the accumulation of further raw materials or else, on the opposite side of the field, are advancing from the physiological outposts to attack specific problems. In spite of the wide separation of these attacking forces there exists between them the best of understanding and the most helpful of communication. There is urgent need that this be the case, for the field is large and the attack must be a prolonged one. With co-operation between different parts of the field and co-ordination of effort throughout the campaign, we can look forward to the daily enjoyment of victory in a conquest which is almost without bounds.

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NOTES ON THE ANCESTRY OF THE BEECH

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The members of the beech family (Fagaceae) rival those of the pine family from a utilitarian point of view, and while of later origin they are equally enshrined in the traditions and poesy of the Anglo-Saxon race and in the practices of innumerable crafts from milling and the manufacture of wood-type to shipbuilding—once a craft but now a disease in its iron age of development.

It will perhaps be possible at some future time to define the demarcation between the beeches, oaks and chestnuts that comprise this great family of Fagaceae and to trace the lines of descent among the hundreds of fossil and living species that are involved. It is easier and less confusing to consider the single line to which the beech belongs, not that there are no great gaps in our knowledge of its geologic history, especially its place in the botanical history of the great area of Asia, but because certain striking conclusions can be deduced from the present state of our knowledge. The beeches (the generic name Fagus is derived from the classical φάγειν, to eat) comprise a fairly compact group of species formerly referred to the single genus *Fagus* (Linné, 1753) well illustrated by the common beeches of Europe, southeastern North America and eastern Asia.

There are four existing species of *Fagus* in the north temperate zone. Two of these occur in the coastal region of eastern Asia. The American beech, formerly much utilized in the manufacture of charcoal, is now largely lumbered for a wide range of special commercial uses such as wooden and laundry ware, handles, clothes pins, shoes, etc., since the wood is hard, tough and strong and does not decay or soften under water. The tree ranges from Nova Scotia westward through Ontario to Wiscon-

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sin and southward to western Florida and Texas. It frequents rich uplands and mountain slopes in the northern part of its range and bottom lands in the South, reaching its maximum development in the lower valley of the Ohio and on the slopes of the southern Alleghanies. The fourth existing species is the European beech and its horticultural varieties. It is one of the common forest trees of temperate Europe from southern Norway and Sweden to the Mediterranean, ascending to elevations of five thousand feet in the Swiss Alps. It is common in southern Russia and throughout Asia Minor to northern Persia.

The common name of beech is from the Anglo-Saxon *boc*, *bece* or *beoce*, the German *buche*, the Swedish *box*—all words signifying book as well as beech and derived from the Sanscrit *boko* or letter and *bokos* or writings. This connection of the vernacular name of the tree with the graphic arts is supposed to have originated from the fact that the old Runic tablets were of beech wood.

The beech has been utilized by the natives of Europe since prehistoric times, a fact shown by the presence of its remains in the deposits of the Swiss lake dwellings of the Neolithic period or younger Stone age. It is one of the largest of British trees, especially on chalky or sandy soils. Beech mast, formerly known as "buck," was not only a subject of medieval local legislation, but it even gives its name to the county of Buckingham.

It is obvious from the interrupted distribution of these four existing species, namely one in Europe, one in southeastern North America and two in eastern Asia, strikingly shown on the accompanying sketch map, that these existing species are the isolated remnants of a distribution which in late geologic time must have covered the intervening areas and embraced practically the whole northern hemisphere. This supposition derived from a study of the present ranges of the four existing species will subsequently be shown to be somewhat less rather than the whole story which geologic history elucidates.

With the exploration of antipodean lands during the last century about a dozen forms of beech-like trees and shrubs were discovered in New Zealand, Australia, Tasmania, Chile and

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Terra del Fuego. Some of these were found to only attain the stature of shrubs, many of them were evergreen and all had tiny leaves. They differ from the northern beeches in their partial lack of deciduous habits, their smaller leaves and in their flowers being solitary or grouped in clusters of three. For a long time these southern forms were referred to the genus *Fagus*, which was divided into two sections—a section *Eufagus* for the well known species of the north temperate zone and a section *Nothofagus* for their antipodean congeners. The latter have since been raised to generic rank, quite rightly it seems to me, although their close relationships and community of origin with the true beeches is clearly demonstrable. The curiously segregated ranges of these existing forms is shown on the accompanying sketch map (fig. 1).

Granting that these two lines are offshoots of a common stock the question of its original home at once suggests itself, along with the query as to whether in some past time members of the two genera flourished side by side either in the north or the south temperate zone. These questions can only be answered by an appeal to the fossil record, a book with unfortunately many missing chapters, especially those relating to the great land mass of Asia.

The oldest known fossil forms are a species (*Fagus prisca* Ettingshausen) from the early Upper Cretaceous (Cenomanian) of Saxony and three species in the Dakota sandstone of the western United States of almost exactly the same age as the Saxon species. Their essentially contemporaneous appearance in Europe and America argues that they were immigrants into both regions from some third area. Only two alternatives are probable. Either their ancestors came from the Arctic region and spread southward simultaneously into Europe and America or else they originated in Asia and spread westward into Europe and eastward into America across the land bridge which closed Behring Sea at about this time. If the Arctic was the original home of the beech its remains should occur in either the Cenomanian or later Cretaceous floras of Greenland where it has not been found although it is present in that region in the Tertiary.

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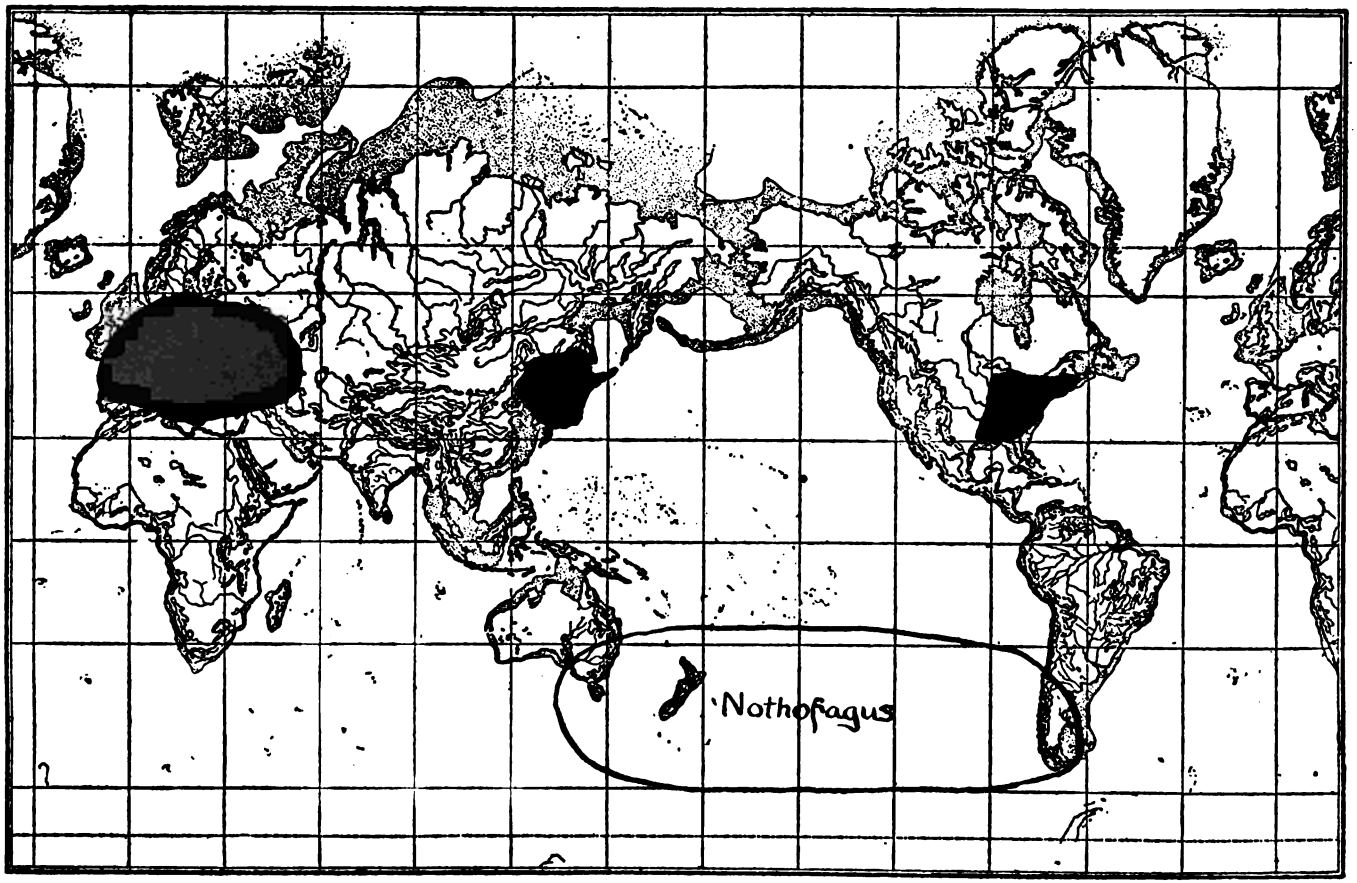

Fig. 1. Sketch map of the world showing the somewhat generalized distributional areas of the recent species of *Fagus* and *Nothofagus*, the former in solid black. Continental borders stippled to the 200-fathom line.

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Furthermore if it had originated in the north it should have been a member of that migratory wave of vegetation that swept southward along the east coast of North America at about the dawn of the Upper Cretaceous. Our east coast Cretaceous contains a very large flora found in deposits of this age from Marthas Vineyard to Alabama and this flora had a great many elements in common with the Greenland Cretaceous flora. No traces of Cretaceous beeches have, however, been discovered along the Atlantic coast.

If, on the other hand, *Fagus* originated in the Asiatic region it would have had an almost latitudinal pathway with broad and uniform land surfaces both westward to Europe and eastward to western North America, the latter region almost entirely cut off from eastern North America by an epicontinental sea (see map, fig. 2). The presence of petrified beech wood in the Cretaceous of Japan, of Germany and in the Eocene of the Caucasus, as well as leaves in the Cretaceous of Vancouver Island and in the Eocene of Alaska and the early Tertiary of Australia would similarly accord with this hypothesis of its center of radiation better than any other.

The Eocene records also embrace various North American and European forms which offer no difficulties on such a theory, nor do the numerous succeeding Oligocene and Miocene species of the northern hemisphere. The antipodean records, of which there are a considerable number, seem at first thought to offer greater difficulties. In deposits the age of which is unfortunately somewhat uncertain but which are either Eocene or Oligocene, four species of *Fagus* are found in southern South America—three in Chile and three in Terra del Fuego and a fifth is found on the edge of the Antarctic continent in Graham Land. They are, in all of these localities, associated with an abundant display of *Nothofagus*, no less than ten species from Chile, Patagonia, Terra del Fuego and Graham Land having been described by Engelhardt and Dusen. The Tertiary species of *Fagus* in the Australian region are likewise associated with four or five species of *Nothofagus*. Another species is found in Tasmania and there are several in the outlying region of New Zealand, one of the latter being common to eastern Australia.

It would be an attractive hypothesis to consider *Fagus* as of

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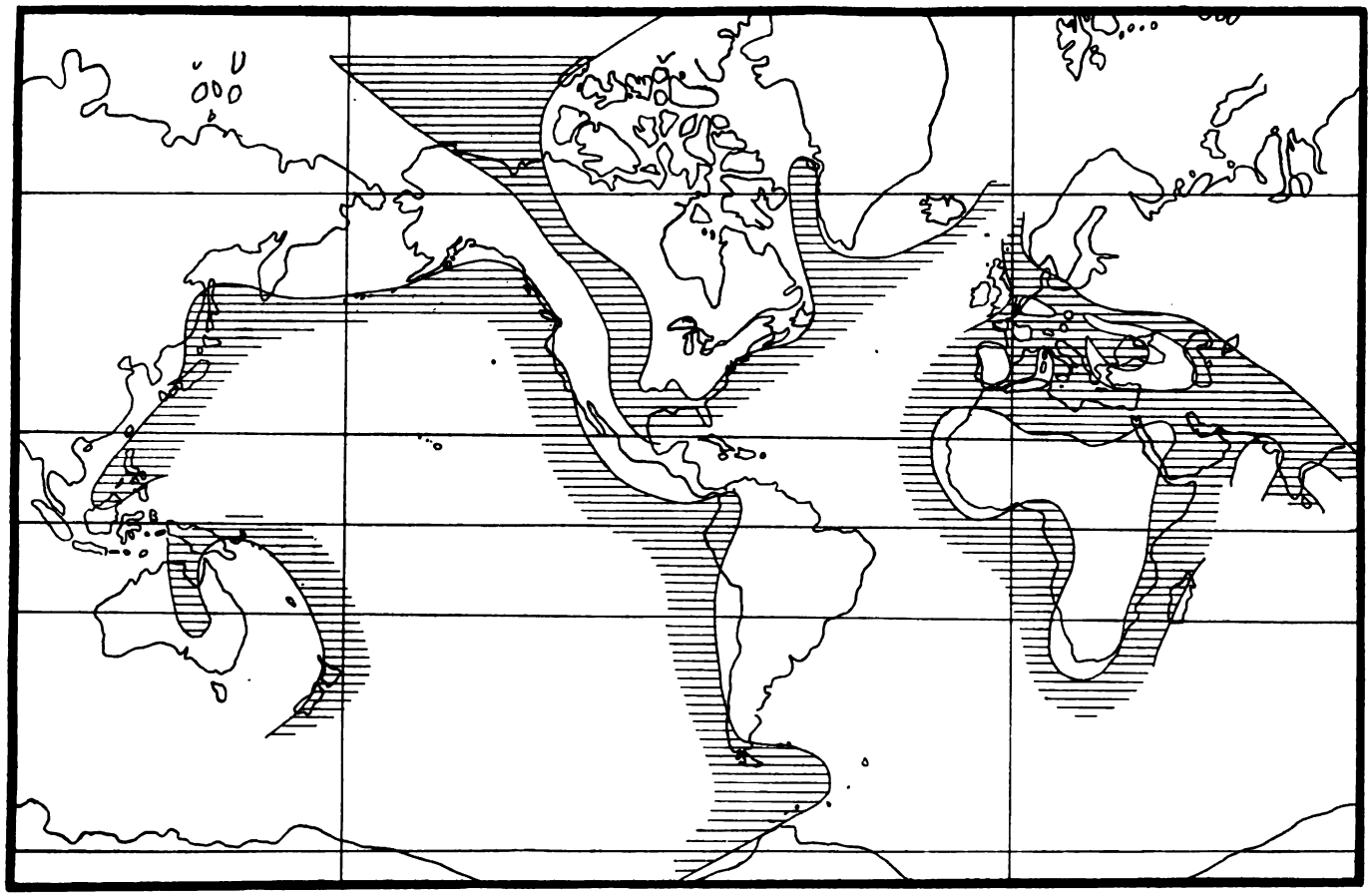

Fig. 2. Map showing strand lines and land connections in early Upper Cretaceous times (Cenomanian).

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northern origin and *Nothofagus* as having originated independently on the broad bosom of the Antarctic continent, from whence it spread northward into southern South America on the one hand, Tasmania and eastern Australia on the other, and to New Zealand by a third route from the south northward. Such a theory would be in accord with many recent discussions of geographical distribution. It would almost certainly be suggested by plant geographers who lacked any knowledge of antecedent floras by the peculiar distribution of the existing species of *Nothofagus*, namely—a dozen very similar species about equally distributed between southern South America (Chile and Terra del Fuego), south Australia and Tasmania, and New Zealand.

This attractive hypothesis is, I believe, entirely erroneous, and for the following reasons:—It would entirely fail to account for the distribution of *Fagus*, which is clearly of northern origin and yet is associated with *Nothofagus* in the Tertiary of South America, Graham Land and Australia. Moreover what appears to be true species of *Nothofagus* occur in the Oligocene of Greece (*Fagus pygmaea* Unger and *Fagus chamaephegos* Unger). If on the other hand *Nothofagus* was of Holarctic origin it would reach these antipodean lands along with *Fagus*. A number of elements of the Dakota sandstone flora (Upper Cretaceous) are found in the later Cretaceous of Argentina, showing that migration from North America into southern South America was not only possible but actually took place during the Upper Cretaceous and all lines of evidence—bathymetric, tectonic, petrographic and paleontologic, indicate that South America was in direct connection with Antarctica. The Australian species would have reached Australia, *Fagus* and *Nothofagus* together or in successive migrations either from southeastern Asia or from Antarctica over the then existing land connections.

New Zealand offers more difficulties but there is a really vast amount of both paleobotanical and botanical evidence (the latter discussed by Alfred Russell Wallace in his Island Life) indicating a common origin for the Australian and New Zealand flora. There may have been a direct interchange of floral elements by way of the now sunken lands indicated by the topography of the ocean bottom, and by the coral islands

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and tectonic lines across Polynesia. It seems probable, however, that Australia and New Zealand were never actually connected in later geologic times, that is to say, since the higher plants were evolved. Otherwise New Zealand should contain some traces of the animals such as the marsupials and plants such as the eucalyptus that particularly characterize Australia. New Zealand has, however, been shown to have been much more extensive in former than it is at the present time and it seems probable that it received its beeches from the Antarctic continent rather than by a land bridge between New Zealand and Australia. These suggested lines of migration are seen to have been possible by referring to the sketch map (fig. 2) which shows the approximate distribution of land and water during the early Upper Cretaceous.

If *Fagus* or even *Nothofagus* were of southern origin, and I think that it will be conceded by botanists familiar with the two genera that they are the immediate descendants of a common stock, it would be contrary to the general rule of past distribution of the ancestors of our existing flora which in every case that has been investigated show former cosmopolitanism in the great land mass of the northern hemisphere and a simultaneous or subsequent migration into southern lands. This statement is notably true of the coniferous genera *Araucaria* and *Dammara*. It is likewise true of the great antipodean families Proteaceae and Myrtaceae, and many other and no less striking instances could be enumerated.

It would seem that *Nothofagus* was more primitive than *Fagus*, or at least that it is more like the original stock from which both took their origin. This stock was probably evergreen in habit, small in size and with relatively reduced leaves. If this supposition is justified it might be considered as furnishing another argument for the northern origin and southward migration of the original stock, for the natural place to look for existing forms most like their remote ancestors has been considered by some students of distribution as being farthest away from the original center of radiation—nearer this center they would tend to have been replaced by successively later and later evolved forms.

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The actual details of the past history of the beeches were of course infinitely more complicated than I have sketched them. All of the new species did not originate successively in one area and radiate from it regularly in all directions. Each continental area must have been a local center of evolution and radiation after the stock had once reached it, and doubtless there were interchanges between one and another parts in progress during the whole of the long ages of the Tertiary period. Nevertheless the foregoing sketch shorn of its unknown and confusing complexities emphasizes the major features of beech evolution and migration.

It remains for me to consider the recorded occurrences of beeches during past time somewhat more fully than I have done in the preceding paragraphs. The Cretaceous species have already been enumerated in the paragraphs discussing the probability of Asia having been the original home of *Fagus* and *Nothofagus*. The Eocene species are nine or ten in number and include records from Europe, Greenland, Alaska and the western United States. The Oligocene species number about fourteen and the records include eastern and southwestern Asia, probably Australia, all the countries of Europe where plants of this age are represented, eastern North America, Graham Land, Chile and Terra del Fuego. The Miocene species number about thirty. *Fagus* at this time was practically cosmopolitan, being represented throughout Europe and North America, particularly in the west in the Rocky mountain province (Colorado) and along the Pacific coast (California) where it has now long been extinct. It was present in Iceland and Spitzbergen, in Australia, and at several points in eastern Asia. The Pliocene species number over a score and include several that foreshadow forms that are present in our recent floras. The records include Japan and most Pliocene plant localities in Europe. In the United States where Pliocene deposits other than those of strictly marine origin (and consequently lacking fossil plants) are very rare, an extinct species of *Fagus* is found in Alabama along the Gulf coast of that period.

Beech forests seem to have flourished in undiminished vigor over most of the northern hemisphere up to the advent of the

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glacial period, although their continuous range had already been interrupted by the formation of mountain ranges like those of the western United States or those of central Asia which by their interference with the climatic equilibrium caused the development of vast stretches of arid or semi-arid country like that of the present day in central and southwestern Asia and in our own western and southwestern states.

The Pleistocene records of the beech include the remains of wood, of an abundance of leaves as well as of nuts and husks, the latter almost always present in buried swamp deposits. These records embrace an extinct species in Japan, remains of the still existing *Fagus japonica*, and other leaves in that country which are distinguished with difficulty from the European beech. The latter, *Fagus sylvatica*, occurs in England, Germany and southern Europe at this time and is often associated with traces of Neolithic man. The American beech, variously denominated (*e.g.*, *Fagus ferruginea* Aiton, *Fagus americana* Sweet, *Fagus atropunicea* (Marsh) Sudworth, and *Fagus grandifolia* Ehrhart), is widespread in Pleistocene deposits. It is found in the Port Kennedy bone cave in Pennsylvania; in the bluffs of the Mississippi in western Kentucky; in the high river terraces of West Virginia, and in buried swamp deposits in Maryland, Virginia, North Carolina and Alabama.

In the foregoing brief sketch I have refrained from saying much about the utility of the beeches or of the surpassing beauty of their light smooth bark and glossy symmetrical foliage. Beech woods are the common heritage of the Anglo-Saxon race and are intimately associated with our ancestors during the time that they were slowly emerging from barbarism. Ages later they furnished the best fuel for the open hearth heating and cooking of our more immediate ancestors and along with the oaks furnished the mast for the swine that roamed the forests of the feudal barons.

The mist of tradition and history that clothes the beech should inevitably awaken some of the thrill corresponding to that awakened by a visit to some scene of ancient romance or tradition such as Kenilworth Castle, Palestine or the scenes of classic Greece or imperial Rome.

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BOOKS AND CURRENT LITERATURE

PERMEABILITY AND ANTAGONISM.—Osterhout is continuing his earlier work upon antagonism and has recently published several articles on the measurement of protoplasmic permeability with reference to various salt solutions and the antagonistic effects of certain pairs of salts on each other. An attempt is made to put the whole matter on a quantitative basis by using exact electric measurements.[1] As heretofore, he employs small disks (13 mm. in diameter) cut from *Laminaria* fronds, these disks being placed together so as to form a cylinder. Through this cylinder of tissue an electric current is passed from end to end and the resistance is measured. The conductance (reciprocal of the resistance) is taken as a measure of protoplasmic permeability. By treating the cylinder of tissue with various salt solutions it is found that one class of substances (those that contain monovalent kations, except H) increases permeability while another class (those that contain bivalent or trivalent kations) decrease it. In the first class belong the chlorides of K, Cs, Rb, Li, NH_4, also other salts such as the bromide, iodide, sulphate and acetate of Na. Examples of the second class are chlorides of Ca, Ba, Sr, nitrates of La, Ce, Y, Th and sulphates of Fe and Al. According to his hypothesis,[2] substances in one class should have an antagonistic action on those of the other, and the degree of antagonism should depend on the extent to which the one substance increases and the other decreases permeability. NaCl increases permeability while $CaCl_2$ decreases it, hence these substances may be expected to antagonize each other with respect to permeability changes and this is found to be true in actual experiment. A number of salts were thus studied and it appears that those with bivalent and trivalent kations[3] act in a greater or less degree, like $CaCl_2$, decreasing permeability.

The question as to whether the changes in permeability thus shown

[1] Osterhout, W. J. V., The permeability of protoplasm to ions and the theory of antagonism. Science n. s. **35**: 112–115. 1915.

[2] Osterhout, W. J. V., On the nature of antagonism. Science n. s. **41**: 255–256. 1915.

[3] Osterhout, W. J. V., On the decrease of permeability due to certain bivalent kations. Bot. Gaz. **59**: 317–330. 1915. *Idem*, The effect of some trivalent and tetravalent kations on permeability. Bot. Gaz. **59**: 464–473. 1915.

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are injurious or not is taken up in another paper.[4] The author finds that the permeability can be either increased or decreased by treatment with proper solutions, and that the tissue soon regains its normal permeability upon being returned to its original medium, sea water in this case. If the tissue is repeatedly transferred from a solution that decreases to one that increases permeability, and back again, being finally brought into sea water, it regains its normal condition without any apparent injury—E. S. JOHNSTON.

ENDEMIC FLORAS AND EVOLUTION.—When the various theories of evolution are put to the test of interpretation of facts in nature the result is generally inconclusive and unsatisfactory. A notable exception is offered by the work of Willis upon the endemic species of Ceylon, which are 809 in number, out of a total plant census of nearly three thousand species.[1] Twenty-three of the 324 genera are of strictly Cingalese distribution; six families of seven species each are entirely endemic; four families with a total of 102 species have 91 of them endemic, and 14 families containing a total of 435 species include 255 which are endemic.

In connection with a discussion of the distributional relationship it is shown that many of these species are extremely localized. Thus *Coleus elongatus* is represented by not more than a dozen individuals on a mountain top, and over a hundred of the endemics are similarly restricted in occurrence, and the group as a whole constitute the rarest plants of the island.

Dr. Willis points out that the various features of occurrence of the endemics constitute "an insuperable objection to the theory of natural selection and adaption." Thus the local species of Ceylon are the rarest, which should not be the case if they had developed in response to local conditions. On the contrary, the author holds that the endemics, as species of local origin, have developed quite indifferently to local conditions. It is concluded that this sensationally large number of endemics owes its origin to mutations which may be almost of generic amplitude. Thus the endemic species do not show any close similarity to their nearest relatives, a fact which the reviewer has previously noted in endemics of the Salton region.—D. T. MACDOUGAL.

[4] Osterhout, W. J. V., Extreme alterations of permeability without injury. Bot. Gaz. **59**: 242–253. 1915.

[1] Willis, J. C. The endemic flora of Ceylon, with reference to geographical distribution and evolution in general. Phil. Trans. Roy Soc., Lond., Ser. B, **206**, pp. 307–342. 1915.

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NOTES AND COMMENT

The report made to the Chief Forester of the United States in regard to the progress of investigative work during 1915 indicates the nature of the results which are being secured at the eight experiment stations of the Forest Service. The importance of the work at these stations has now been fully demonstrated, both by the solution of many small problems and by the progress which is being made in the investigation of some of the larger and more difficult problems in the management of the forest crop. Field examinations are coming to be more and more supplemented by instrumental and laboratory work, and the distinctive character of the various western National Forests has done much to increase the volume of this work which is now engaging the twenty-seven men who form the collective staff of the eight stations.

Studies in artificial methods of seed extraction have been continued, and the effect of the source of seed upon the character of the resulting stock has been investigated in Douglas fir. The discovery that seed production is low in young and old trees has thrown light upon the age and number of trees that should be left for the reseeding of lumbered tracts. A study of some 6000 acres formerly planted to young nursery-grown trees in the Pacific northwest has given valuable guidance for future plantings in that region. For the western white and yellow pines seeding is more successful than transplantation, while the opposite is true of western larch. A study of reforestation in old burns of Douglas fir west of the Cascades has shown that only the most severe fires destroy all of the tree seeds in the litter which covered the forest floor. The seed of the western white pine is able to resist injury from fire better than the seeds of any of its associates. After a fire which is not severe enough to destroy all tree seeds the earliest stages of reforestation in the Cascade region are formed by the same species that constituted the original forest, but by different proportions of them. The study of the effect of a forest cover upon erosion and stream flow has been continued at the Wagon Wheel Gap station, in Colorado, and in a short time one of the watersheds will be denuded, in order to secure a comparison with its former behavior and with the simultaneous behavior of the watershed remaining in forest. The instrumental

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study of climatic conditions is being carried on in thirteen localities in Colorado, California and Idaho, with a view to correlating the climatic characteristics with the different forest types which occupy these places. Studies are also in progress on the growth, behavior and management of a number of important commercial trees. Various economic and statistical studies have been carried out; 1800 records of occurrence were added to the distribution data which are being collected; and numerous minor activities were carried on.

The year 1915 witnessed the establishment of a Branch of Research in the Forest Service, which brings under one administrative direction all of the investigative operations that are being carried on at the experiment stations and at the Forest Products Laboratory at Madison, as well as the investigations in grazing problems, and the recording of distributional data.

Dr. Howard H. M. Bowman, of the University of Pennsylvania, reports (Science, **43**: 244) the finding of two species of seed-plants at depths of 96 and 108 feet in the Gulf of Mexico, near the Dry Tortugas. The plants in question are species of *Halophila*, belonging to the wholly aquatic family Hydrocharidaceae. Their occurrence at this depth probably establishes a new record in the bathic distribution of flowering plants, and is of great interest, even if we prefer not to accompany Dr. Bowman in his conclusion that he has hereby discovered some additional evidence for the subsidence of the floor of the Gulf in that vicinity.

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A CRITIQUE OF THE HYPOTHESIS OF THE LIME-MAGNESIA RATIO

I

CHARLES B. LIPMAN

University of California, Berkeley, Cal.

The time has come for agronomists, soil specialists, and plant physiologists to scrutinize with a critical eye the whole situation with respect to the subject of the lime-magnesia ratio in soils and its relation to crop production. Much, too much, has already been said and done on this subject in a practical way, affecting the operations and ideas of farmers, to make it safe for us to go on piling up discussions with respect to it without pausing to look back over all of our results and determine their significance as appears rational in the light of the work thus far done. This should be done at least to correct misimpressions and for the purpose of formulating a clear and concise statement, based on the best information which we have, to serve as a guide for the rational man. The writer has therefore taken the liberty of bringing together for the inspection of his colleagues, a review of the results thus far obtained by investigators of this interesting subject, and ventures in addition such critical remarks with reference to them as appear, from close study and thought as well as from his own experimental data, to be justified. That the past and present status of the question in hand have been rather alarming from their effects on soil management in certain quarters is not stated above on the basis of hearsay. I have known of measures employed in soil management in this state, based on the theory of the lime-magnesia ratio as first enunciated by Loew and later exploited by unscientific men, which to the rational-minded experimenter with soils and plants, appear to be the veriest folly. Such should not be allowed to go on, without

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the statement in public, and soon, of some definite information free from all bias, with respect to the whole matter.

The lime-magnesia ratio hypothesis of Loew was an outgrowth of studies made by Loew and by Böhm before him on the functions of lime and magnesia in plant nutrition and growth. Loew became so impressed with the reversal of conditions among other things, regarding the quantitative occurrence of lime and magnesia in the seeds and in the straw of plants respectively that he continued his experiments with a view to ascertaining if it was necessary for lime and magnesia to bear a certain ratio to each other in the medium of plant growth in order to insure normal development. As a result of these investigations Loew was led to formulate[1] what has since come to be the celebrated lime-magnesia ratio hypothesis, which bears his name. According to this hypothesis, either lime or magnesia is toxic to plants when found in the medium of growth in large excess of the other; that either of these substances will neutralize in part or in whole the deleterious effects of the excess of the other; that different plants require slightly different CaO: MgO ratios, and, to illustrate, that such ratios should be 1: 1 CaO: MgO for oats, 2: 1 CaO: MgO for barley and 3: 1 CaO: MgO for buckwheat. As subsidiary to these important phases of the theory, Loew claims that both lime and magnesia should be determined in soils by our regular acid extraction methods of analysis in order that information may be obtained with reference to the lime-magnesia ratio in them, and, also, that the form in which lime and magnesia are found in soils may affect to a considerable degree, the activity of each, and hence the nature of the necessary ratio in every case. Many of these additional observations of course resulted from investigations of Loew and others carried out subsequently to those above cited. In the latter there are pointed out the functions of calcium and magnesium, showing that calcium cannot replace magnesium in its work of carrying phosphoric acid to the seed and that conversely magnesium cannot take the place of calcium in the work of the latter as a "carbohydrate carrier" in

[1] Flora, 1892, p. 368.

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the chlorophyll bearing parts of plants. Without going into them here, it suffices to say that ample evidence is furnished as a basis for such conclusions and explanations as are given for the earlier observations of Böhm, Räumer and Kellerman.

With these ideas as a basis, Loew and his co-workers or pupils in various parts of the world, proceed to gather experimental data in support of the hypothesis thus indicated. It is a review of these investigations as well as of those of other investigators working entirely independently of Loew which I propose to give here briefly. No attempt is made below to review all of the investigations which have a bearing on the question of the lime-magnesia ratio, but all important and typical investigations are adverted to so far as the higher plants are concerned. The lower organisms are merely mentioned when necessary for the elucidation or emphasis of principles and facts appertaining, in the main, to the higher plants. It is further to be noted that the investigations here considered are discussed in groups as follows: I. Positive, or those supporting Loew's hypothesis; II. Negative, or those showing little or no support for its tenability; and III. Indifferent, or those which are related to the subject of the functions of lime and magnesia in plant growth, but giving little or no evidence either in support or contradiction of the hypothesis in question. Obviously the lines in such classification must at least in some instances, be arbitrarily drawn and particularly as between the first two classes and the last, nevertheless, the classification serves the purpose of bringing into sharp relief certain phases of the present status of the subject which can scarcely be considered as being affected by the drawing of the lines as indicated.

THE POSITIVE INVESTIGATIONS, OR THOSE GIVING SUPPORT TO THE LIME-MAGNESIA RATIO HYPOTHESIS

The investigations to be referred to under this head represent those undertaken by Loew and others to test the principle enunciated by the former, not only in the paper above specifically cited, but also in several others in which the function of the mineral nutrients and especially of calcium and magnesium in plant

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nutrition are discussed. These papers are either referred to specifically in the bibliography herewith submitted or are cited in certain of the publications mentioned therein. It is not necessary to mention them now, more in detail, since they merely iterate and reiterate the now accepted facts first pointed out by Loew with regard to the essential relationship of calcium to the nucleo-proteids and the specificity of its functions with regard thereto, and with regard to the similar relationship of magnesium to the translocation of phosphorus in the plant. The details of these excellent investigations and explanations are too well known to my colleagues to require repetition here.

In 1901 Loew and May[2] carried out a series of investigations in support of the lime-magnesia ratio hypothesis of the former. Water, sand, and soil cultures were employed and the plants grown were cowpeas, privet, tobacco, barley, oats, wheat and beans. The nitrate, sulphate, and carbonate of each calcium and magnesium were tested. The authors found that magnesium is poisonous to plants when it occurs in great excess over lime, the plants showing under its influence symptoms of starvation. The addition of an excess of calcium counteracts the noxious effects of magnesium and with a proper ratio of the two bases, the abnormal nutrition of the plant is obviated. It was further claimed by these authors that the best ratio of *soluble* lime to *soluble* magnesia for the germination and growth of plants is 5:4 on the basis of molecular weight, and 7:4 on the basis of actual weight. They appear also to have found that the more soluble magnesium compounds, like the nitrate and sulphate are more toxic than the less soluble forms and that the more soluble compounds of lime are more efficient as antagonistic agents to the toxicity of magnesia than the less soluble forms. With these results as a basis, Loew and May draw conclusions for use in practical soil management and formulate directions for liming soils.

In further support of the foregoing investigations of Loew and of Loew and May, investigations were carried out under the in-

[2] Bul. 1, Bur. Pl. Ind. U. S. D. A., 1901.

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spiration of the former by T. Furuta and K. Aso, dealing with the subject of the proper ratio of lime to magnesia for various plants. Furuta[3] found when working with soil mixtures in which there were fixed ratios of lime to magnesia, that the necessary ratios vary from 3 of lime to 1 of magnesia, and from 1 of lime to 2 of magnesia with such crops as cabbage, buckwheat, and oats. Furuta makes the claim that in plants producing heavy foliage, the ratio should be 3 to 1, whereas for plants with smaller leaf surfaces, like those of the cereals, a ratio of 1 to 1 is desirable.

Three papers have appeared from the pen of K. Aso. In the first[4] of these, examples are given of the unfavorable effects in laboratory experiments obtained with improper ratios of lime and magnesia, allowing of the excess either of lime or of magnesia. The ratio for favorable growth is indicated for barley, soy beans, and onions. The claim is further made that calcium and magnesium in soils should be determined so that their amounts may be known in the practical management of soils and not only that the total forms of lime and magnesia should be determined, but that the "available" quantities of these materials, should be ascertained. When soils are limed these figures, according to Aso, should be borne in mind. That author also points out the markedly poisonous effects of magnesium oxide in the absence of lime, and the influence that the latter exerts in increasing the number of root hairs and therefore the total absorbing surface of the root.

In the second paper[5] the mulberry tree instead of rice was studied in a similar way. The experiments with that plant are said to indicate that the normal development of the mulberry tree depends to a considerable extent on the lime-magnesia ratio of the soil. Here again pot experiments were employed and ratios of lime to magnesia were made to vary between 1 to 3 and 4 to 1. The net result is claimed to have been the establishment of a ratio of 2 to 1, as the proper one for the mulberry tree. Ex-

[3] Bul. Col. Agr. Tokyo, Japan, vol. 4, p. 371, 1902.
[4] Bul. Col. Agr. Tokyo, Japan, vol. 4, p. 361, 1902.
[5] Bul. Col. Agr. Tokyo, Japan, vol. 5, p. 495, 1903.

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cess of magnesia over lime was found to retard growth, small leaves being obtained, though no symptoms of dwarfing disease were noted.

In the third paper,[6] Aso describes a specific study of the subject of the lime-magnesia ratio as affecting rice. This work was carried out in pot experiments from which it is claimed that the "lime factor" of Loew, so far as rice is concerned, agrees with that of other Gramineae, or in other words, is between 1 and 2. It is further noted that rice shows a relatively high resistance to an excess of magnesium carbonate and that the latter does not depress the yield of rice so much as does an excess of lime. Maximum yields, according to this investigation, depend to a very great degree, on the maintenance of the proper ratio of 1 to 1.

About the same time other Japanese investigators busied themselves with the subject of the lime-magnesia ratio. These investigations were, evidently, all inspired by the work of Loew himself, in Japan. The first of these which may be reviewed here is that of Daikuhara,[7] who grew beans in pots adding lime and magnesia in varying quantities to the soil. As a result of these experiments he claims to have found that in the growth of the bean prior to the fruiting stage, a ratio of 2 of lime to 1 of magnesia gives the best results. The criteria employed were vigor of plant, height of stems and size of leaves.

Nakamura[8] carried out pot experiments with barley. He used a natural soil which contained seventeen times as much lime as magnesia, both being determined by the strong hydrochloric acid digestion method. He added to this soil varying quantities of magnesium sulphate from one-twenty-fifth to one-fifth of the amount necessary to make the quantity of magnesia in the soil equal to that of the lime. He found that the amount of magnesia which was equivalent to 88.82 grams per pot, as against 170 grams of lime, or a ratio of 2 of lime to 1 of magnesia, gave the best results.

In 1905 to 1906 another series of investigations was published

[6] Jour. Col. Agr. Tokyo, Japan, vol. 6, p. 97, 1904.
[7] Bul. Col. Agr. Tokyo, Japan, vol. 5, p. 501, 1903.
[8] Landw. Jahrb., vol. 34, p. 141.

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by some of the same investigators whose work has just been reviewed. Loew,[9] together with Aso, published a paper on the different degrees of availability of plant nutrients in which the statement is made that Loew's hypothesis of the lime-magnesia ratio is predicated on an equal availability of the two bases and that the ratio changes with the availability of the bases, because more of the base will enter the plant when the compound is more available. Thus the ratio of the bases which is offered to the roots is different from that which is found in the plant. In these investigations it was also found that magnesia in the "burnt" form was more available than in the form of pulverized magnesite, and that magnesium sulphate is still more available than the first. The authors arrange for an "agronomical equivalent" which represents the amount of easily available forms of lime and magnesia which are equivalent to 100 parts of the natural calcium and magnesium carbonates in the form of the finest powder. They explain that calcium carbonate acts differently from gypsum in the soil because the latter has a low degree of availability since dilute acids do not make it more soluble. Therefore, the claim is made that even large applications of gypsum do not essentially alter the lime content of the leaves, and an excess of gypsum is not so injurious therefore, as an excess of calcium carbonate. Finally, the claim is made that decrease in harvest which follows the liming of some soils, is due rather to the production of a bad ratio between lime and magnesia than to decreasing the available phosphoric acid supply.

Daikuhara,[10] again, in a study of barley, found that the yield of that crop is doubled on well manured soil by making the ratio of lime to magnesia 1 to 1 through the addition of more lime, since the natural soil with which he worked contained lime to magnesia as 0.34 to 1. The yield was even more than doubled when the fertilization was one-sided, or when no application of fertilizers at all was made. The actual percentages of lime and

[9] Bul. Col. Agr. Tokyo, Japan, vol. 6, p. 335. Cited from E. S. R., vol. 17, p. 121, 1905–06.

[10] Bul. Imp. Cent. Agr. Ex. Sta. Japan, vol. 1, p. 13. Cited from E. S. R., vol. 17, p. 1149, 1905–06.

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magnesia in this soil were 1.64% calcium oxide and 1.91% magnesium oxide.

Daikuhara[11] found in pot experiments with rice instead of barley, that when magnesia is applied as magnesium sulphate in crystalline form, so little of it is needed in the presence of lime for paddy rice in sand cultures, that the best ratio is 3 : 1 of CaO: MgO, while in the form of natural calcium and magnesium carbonates, the best ratio is 1: 1, as claimed by Aso. It is further stated that the conclusions thus drawn will hold good for sandy soils while for clay soils the ratios of lime as carbonate to magnesia as sulphate are doubled.

Daikuhara[12] also continued his work with the tobacco plant. The plants were here again grown in pots and various ratios of lime to magnesia were tried. A ratio of 4: 1 (CaO:MgO) was found to be the best. In all cases the application of lime benefited the tobacco plants.

Several other Japanese investigators in the following two or three years occupied themselves with the same question and the results of all of their experiments may be said in brief, to be confirmatory in nature of those obtained by Loew, his co-workers, and his pupils, as above described. For example, Suzuki[13] carried out a series of pot experiments which emphasized particularly the injurious effect of an excess of lime when applied to the soil. He shows among other things that large amounts of lime depress the availability of phosphoric acid for rice, even when phosphoric acid is applied in the very soluble form of secondary sodium phosphate. Calcium carbonate under these conditions, when applied in excess depresses the yields, while, on the other hand, under some conditions, calcium sulphate increased the yields, hence the conclusion above indicated is drawn. When powdered magnesite was applied to the soil, making a ratio of CaO:MgO equivalent to 1: 3, the yield was greatly depressed.

[11] Bul. Imp. Cent. Agr. Ex. Sta. Japan, vol. 1, p. 23. Cited from E. S. R., vol. 17, p. 1152, 1905–06.

[12] Bul. Imp. Cent. Agr. Ex. Sta. Japan, vol. 1, p. 17. Cited from E. S. R., vol. 17. p. 1153, 1905–06.

[13] Bul. Col. Agr. Tokyo, Japan, vol. 6, p. 347.

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Bearing on the same subject Maki and Tanaka[14] attempted to bring back to good producing condition a soil which they call "overlimed." In doing so they grew barley in pot experiments and treated the soil with varying quantities of magnesium in the form of magnesium sulphate. Their work seems to indicate that one-twentieth as much magnesia in that form is needed to bring an overlimed soil into good condition as is necessary of magnesia in the form of magnesite.

Namikawa[15] carried out investigations on the "lime factor" for flax and spinach and found that the best ratio of lime to magnesia for these two crops was 1:1. The experiments were simultaneously carried out with those in the foregoing investigations which have just been discussed.

Like Aso, Nakamura[16] found in pot experiments with the mulberry that a proper ratio of lime to magnesia is necessary for the favorable development of that tree. He found that 3:1 (CaO: MgO) was necessary.

In work carried out about the same time, Kanomoto[17] found in working with oats, rice, barley, buckwheat, mustard and onions, even more strikingly positive results than other Japanese investigators above cited who worked with similar crops, again emphasizing, according to that investigator, the necessity of the proper lime-magnesia ratio for the proper development of those plants. Confirming the work of Kanomoto, Sirker[18] found that the ratio of lime to magnesia for oats was 1:1, in a series of investigations carried out in Japan.

Contemporaneous with the last investigations reviewed were those of Bernardini, reported in two papers, one in joint author-

[14] Bul. Col. Agr. Tokyo, Japan, vol. 7, p. 61. Cited from E. S. R., vol. 18, p. 14, 1906–07.

[15] Bul. Col. Agr. Tokyo, Japan, vol. 7, p. 57. Cited from E. S. R., vol. 18, p. 32, 1906–07.

[16] Bul. Imp. Cent. Agr. Exp. Sta. Tokyo, Japan, vol. 1, p. 129. Cited from E. S. R., vol. 19, p. 102, 1907–08.

[17] Bul. Col. Agr. Tokyo, Japan, vol. 7, p. 599. Cited from E. S. R., vol. 20, p. 321, 1908–09.

[18] Chem. Abst., vol. 4, p. 48. Cited from E. S. R., vol. 21, p. 624, 1909.

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ship with Corso[19] and the other with Siniscalchi.[20] In the first of these papers, an account was given of experiments which are said to confirm the work of Loew and the Japanese investigators which is above reviewed. The best ratio for wheat, rye, oats, rice, and barley is said to have been 1:1 (CaO:MgO), whereas 2:1 (CaO:MgO) was best for maize, onions, spinach, flax and cabbage. For the Leguminosae 3:1 (CaO:MgO) was shown to be the best.

In the second paper, experiments are reported with optimum nutritive solutions and pot cultures. From the solution work, which constituted a continuation of Bernardini's previous work, the conclusion is drawn that phosphoric acid absorption by plants depends on the lime-magnesia ratio. As the ratio increases in favor of the lime, phosphoric acid assimilation decreases and vice versa. From the pot cultures in which lupines were studied, the conclusion is drawn that not the absolute, but the relative or proportionate amount of lime and magnesia are responsible for toxicity, or lack of it, owing to the fact that the two ions are absorbed by the plants in the same ratio as they are present in the soil.

In 1911 Warthiadi[21] published a dissertation on the "variation of plants under the influence of lime and magnesia." The work was carried out in both solution and sand cultures. Warthiadi claims to have confirmed the findings of Loew and Willstätter, according to which an excesss of magnesia injuriously affects the yield of straw, whereas an excess of lime similarly affects the yield of grain. Warthiadi also discusses other physiological factors which are concerned with the assimilation of the chemical elements essential to plant growth and finally concludes by supporting the idea that there is a necessity for a ratio of 1:1 (CaO:MgO) in growing cereals.

[19] Ann. R. Scuola, Sup. Agr. Portici, vol. 7, p. 16. Cited from E. S. R., vol. 21, p. 30, 1909.

[20] Ann. R. Scuola, Sup. Agr. Portici, vol. 8, p. 19. Cited from E. S. R., vol. 22, p. 433, 1910.

[21] Diss. R. Tech. Hochschule München, 1911, p. 35.

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From another standpoint Robert Stewart[22] discusses the problem of Loew's lime-magnesia ratio. He gives consideration to analyses of the soils of the Utah Agricultural Experiment Station tract, in certain of which the content of calcium carbonate amounts to 30 to 41% whereas the content of magnesium carbonate varies from 11 to 20% down to a depth of eight feet. These soils had been cropped at the time Stewart wrote, for forty years without manuring. The author claims that because of the fact that no toxic effect has been visible in these lands so far as crops are concerned, that the lime-magnesia ratio, which in this case is about 3:1, is the factor which prevents such toxic effects. He believes that the calcium and magnesium are found there in the double salt form $CaMg(CO_3)_2$ and that therefore magnesium carbonate alone is present in small quantity, and can not be harmful. He refers to the possibility of the different effects which might be brought about by either calcium carbonate or magnesium carbonate alone, as against the effect of the double salt just referred to. For that reason it seems wise to Stewart that magnesian limestone be employed for correcting soil acidity.

At about the same time that Stewart's paper appeared, there was published the report of J. A. Voelcker[23] of the Woburn Agricultural Experiment Station in England. In pot experiments covering a long period, it was found that the addition of magnesia was beneficial to the growth of wheat, provided it never exceeded the ratio of 1 : 1 to the lime content. When added beyond that, the magnesia is toxic. Grain soils containing an excess of magnesia, according to Voelcker, are benefited by a lime application, but lime, on the other hand, in excess, is not toxic like magnesia. Both lime and magnesia were found to affect the general growth of the plant and the root development, and they are said to induce a greener color to the flag and a higher nitrogen content in the grain.

In concluding these investigations favorable to the hypothesis of the lime-magnesia ratio, and before proceeding to a review of

[22] Jour. of Ind. Eng. Chem., vol. 3, p. 376. Cited from E. S. R., vol. 26, p. 723, 1912.

[23] Jour. Roy. Soc. Eng., vol. 73, entire Ser., p. 325, 1912.

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the negative experiments, it may be added that the experiments of Voelcker just referred to have been further amplified and emphasized in the following report of the Royal Society, Volume 74. These, and other investigations, have all tended to confirm the hypothesis of the lime-magnesia ratio. Loew[24] has even gone so far as to suggest that anaemia and other physiological troubles in animals and man observed in Porto Rico, are due in part to a deficiency of lime in the food products, and especially in rice.

THE NEGATIVE INVESTIGATIONS, OR THOSE SHOWING LITTLE OR NO SUPPORT FOR THE LIME-MAGNESIA RATIO HYPOTHESIS

In 1901 von Portheim[25] reported a study after the fashion of Loew's earlier experiments of the rôle of lime in the growth of certain plants. He concludes from these experiments that the presence or absence of lime is immaterial for the seedlings of cress, sorrel, rye, barley, wheat, oats, larch and pine. He points out, however, that when certain untoward influences affect these seedlings, the presence or absence of lime may determine the rate and degree of injury. For example, when lime is absent, the effects of heat on seedlings are noted to be much more serious than in its presence.

In 1903 Gössel[26] carried out a series of investigations with water cultures and soil cutlures. The plants which he experimented with—barley and horse beans—were found to grow well with more magnesium present in the culture than calcium. The highest yields in water cultures were obtained with 0.4 part of lime to 1 part of magnesia. This is a reversal of, and contrary to the ratio which Loew claims to have established. In passing, it may be said here that Loew[27] objects to the experiments of Gössel on the ground that the latter used secondary potassium phosphate in his experiments as a source of potash and phosphoric acid, whereas Loew used the primary form. The objec-

[24] Rpt. Physiologists, Porto Rico, p. 13–17, 1913.
[25] Sitzber. K. Akad. Wiss. Math. Naturw. Cl. Vienna, vol. 110[1], p. 113.
[26] Chem. Ztg., vol. 27, p. 952. Cited from E. S. R., vol. 15, p. 564, 1903–04.
[27] Chem. Ztg., vol. 27, p. 1221. Cited from E. S. R., vol. 15, p. 760, 1903–04.

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tion is made on the ground that the secondary potassium phosphate reduced the injurious effects of an excess of magnesium. It is seen here that Loew admits inferentially the efficacy of other factors than the calcium and magnesium to carry out antagonistic effects. This point will, however, be discussed more fully below.

Dojarenko[28] prepared a statement based on experimental work in the field with reference to Loew's hypothesis on the rôle of lime in soils. The results obtained by this investigator show that the beneficial effect of lime can not entirely be due to its antagonism for an excess of magnesia. The marked benefit obtained with lime applications, with oats, for example, on soils already containing more than enough to neutralize the effects of magnesia according to Loew's hypothesis, would seem to offer proof in that regard.

Meyer has published at least two papers which deal with the question of the lime-magnesia ratio. The first one[29] reports investigations of different forms of lime and magnesia, and the second[30] further experiments with lime and magnesia. In the first, pot experiments were carried out in which no very close relationship could be noted between the maximum yields obtained and the ratio of lime to magnesia existing in the soil. It is true that wherever an insufficient amount of lime is present the yield can be increased by applying either lime or magnesia. The lime requirement is determined by ascertaining the amount of lime in the soil and serves as a useful guide except in soils which are very rich in magnesium carbonate. It was found that applications of magnesia lowered the lime content of the plant and raised the magnesia content thereof. With lime applied, the reverse was found to be true. With the different plants tried in the investigations, there appears to be a great diversity in behavior toward an excess of magnesia. In the later experiments above cited, the work was again carried out in pots with clay loam, sand, and loam as culture media. When in

[28] Russ. Jour. Exp. Landw., vol. 4, p. 183.
[29] Landw. Jahrb., vol. 33, p. 371.
[30] Landw. Jahrb., vol. 39, p. 254. Cited from E. S. R., vol. 23, p. 134, 1911.

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these soils correction was made of the excess of magnesia, reduced yields of both buckwheat and oats followed. When magnesium sulphate, magnesium chloride and sodium chloride were applied to soils with a high magnesia content, they gave increased yields with cereals, though not with hoed crops and the forage plants. Both calcium carbonate and magnesium carbonate slightly increased the yield of red clover, mustard and potatoes on an acid soil deficient in lime, whereas gypsum reduced the yield.

Meyer's investigations are called in question by Loew[31] on the ground that too many plants were grown in one pot to allow of normal conditions for growth and that the plants were harvested in the blooming stage instead of being allowed to mature. He quotes the experiments of other investigators which are above reviewed in support of the contention that the lime-magnesia ratio is an established fact.

In more detailed and careful work than that carried out by most investigators, Konovalov,[32] in a large series of sand and water culture experiments, shows that sand cultures with a nutritive solution supplied increase in producing capacity for both millet and oats with the increase in the supply of lime, the quantity of magnesia remaining throughout constant. This remains true until the ratio of lime to magnesia is as 6.7 : 1. Beyond this ratio, or when the lime is proportionately higher than therein indicated, the yield of millet is somewhat decreased and that of barley considerably decreased. In further sand cultures with barley, likewise, no support for a definite lime-magnesia ratio was obtained. In his water culture experiments Konovalov found that the best yield of barley and maize was obtained with a ratio of 3.3 : 1 and 0.8 : 1 respectively for the yields of above ground parts and total yields. So far as the root yields of barley were concerned, the best ratios were respectively 6.7 : 1 and 13.3 : 1; and for corn roots 3.3 : 1.

In later investigations[33] by the same experimenter, which were

[31] Landw. Jahrb., vol. 39, p. 1005. Cited from E. S. R., vol. 24, p. 716. 1911.

[32] Russ. Jour. Expt. Landw., vol. 8, p. 257. Cited from E. S. R., vol. 19, p. 827, 1907–08.

[33] Russ. Jour. Expt. Landw., vol. 10, p. 303. Cited from E. S. R., vol. 22, p. 433, 1910.

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intended as a continuation of his former work, similar methods were employed with water and sand cultures of wheat, lupines, *Setaria italica* and oats. The results with these confirmed Konovalov's former results. Magnesia alone was found to be injurious to plants and the yields were found to increase with the increase in the lime content of the culture medium. In brief, the author is of the opinion that the results do not lend any support to, and probably deny Loew's view that there is a definite lime-magnesia ratio for every plant.

Somewhat less in the nature of direct evidence against the lime-magnesia ratio hypothesis, are the results of Kossovich and Althausen.[34] These investigators found that barley was benefitted by liming and withstood excessive quantities of calcium carbonate quite well. The injurious effects of calcium carbonate when apparent, would seem to carry over for the second season. Basic magnesium carbonate was found to be the most injurious of all the materials tried. Unfortunately, there is not sufficient evidence given as to the lime and magnesia ratios in the soils employed to allow one to appraise in their true light the results just referred to.

Of similar nature is the statement made by Wheeler and Hartwell[35] in which the value of magnesia as a manure is discussed. The authors incline to the opinion that their experiments indicate that too much attention has been paid by writers to Lowe's theory in their recommendations for the use of magnesian limestone. They put forward the unanswered argument that the effects of any such applications might be explained in other ways than by Loew's theory. In general, they do not believe that the state of our knowledge of the subject justifies us in stating what the ratios of lime and magnesia in soils should be, because soils differ very much in all respects.

In a critical review of all investigations on the subject of Loew's theory regarding the lime-magnesia ratio in soils, Ruijter de

[34] Russ. Jour. Expt. Landw., vol. 10, p. 693. Cited from E. S. R., vol. 23, p. 226, 1910.

[35] Rhode Island Agr. Exp. Sta. Rpt., 1904, p. 221.

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Wildt[36] reaches the conclusion that these reported investigations do not demonstrate the need of a definite lime-magnesia ratio, It is not denied that some relation may exist between some such ratio and plant growth, but that the evidence extant does not support such a view.

In the investigations later carried out by Lemmermann, Einecke and Fischer[37] and by Lemmermann, Foerster and Einecke[38] no support was found for Loew's lime-magnesia ratio hypothesis. In the first paper cited results are given of a large number of experiments carried out during 1907, 1908 and 1909, with six soil types and with eight different crops. The effects on both plants and soil bacteria were studied. No effects were noted so far as the yields were concerned with variations within wide limits in the proportion of lime to magnesia in the soils mentioned. Different plants varied considerably in their behavior to lime and magnesia. Sometimes improvement was noted following upon the application of lime and magnesia, even when those materials were found in the soil to a very slight extent for example, a few hundredths of 1%; sometimes no improvement was noted. Lime, magnesia, and phosphoric acid in their content in plants varied greatly with substantially the same yield of crop. In passing, it may be added that as in the case of higher plants no distinct relationship between lime and magnesia could be established as particularly favorable to the soil bacteria.

In the second publication above cited "there was no constant relation" found "between the lime assimilated by plants and that soluble in the soil solution." Only 4% of the lime in the soil solution was absorbed and about 5.6% of the lime fertilizer.

In 1912 Gile began the publication of a series of papers which have made a notable contribution to the subject here under consideration. In the first paper[39] the relation of calcareous

[36] Cultura, vol. 18, p. 463, 505, 557, 650. Cited from E. S. R., vol. 18, p. 532, 1906–07.

[37] Landw. Jahrb., vol. 40, p. 173. Cited from E. S. R., vol. 25, p. 725, 1911.

[38] Landw. Jahrb., vol. 40, p. 255. Cited from E. S. R., vol. 25, p. 725, 1911.

[39] Porto Rico Agr. Exp. Sta. Bul. 11, 1912.

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soils to pineapple chlorosis was studied. By means of pot experiments and a chemical survey of the pineapple soils, the general conclusion was arrived at that an excessive amount of calcium carbonate in the soil was inducing chlorosis of pineapples. It was found that even 2% of calcium carbonate renders an ordinary sandy soil unfit for pineapples, but on the other hand that soils may contain as much as 40% of calcium carbonate and still grow good plants if the soil consists largely of organic matter. Fertilizer applications were not successful in curing chlorosis, but iron salts applied to leaves or crystals of ferrous sulphate applied to the roots, were instrumental in bringing about normal growth. Gile could find no support for the idea that either the alkalinity of calcareous soils, or large quantities of assimilable lime was the cause of the trouble, but rather believes that the combination of the two which are responsible for the disturbance in the mineral nutrition of the plant by preventing the assimilation of iron, is responsible for the difficulty. A low iron content is always found in the ash and thus lends some support to this view. Plants may show a high lime content in the ash, yet may never have shown during their growth symptoms of chlorosis. In brief, it would appear that these investigations support the idea that an excessive amount of lime, when made soluble and therefore assimilable by the roots of pineapples, like excessive amounts of other soluble materials, may seriously interfere with growth, but these investigations do not show that any relationship is evident here between the bad plant condition and the need of a proper lime-magnesia ratio.

In the second paper[40] a discussion of other experiments is given in which rice is the crop plant employed. The rice was grown in culture solutions for forty and fifty days. Varying amounts of calcium chloride and magnesium chloride were added to the nutrient solution. These were used in a large variety of ratios in order to discover if possible if a certain ratio was most favorable to the growth of rice. An attempt was also made to study, besides this one question, that of the concentration of the solution in its relationship with the growth of the rice plants.

[40] Bul. 12, Porto Rico Sta., 1913.

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The general conclusion reached by Gile is that an excess of lime or magnesia is toxic, not simply because of the ratio between those two materials, but because of the improper balance between each of them, or both, and all the other salts present. The problem therefore, as it appears to confront Gile, is not merely the simple one of balancing the lime and magnesia between themselves, but also of balancing all other salts in a nutrient medium with the lime and magnesia. This interesting deduction made by Gile is again very strikingly brought out by the investigations of Tottingham,[41] which indicate that not so much the ratio between the magnesium and calcium, but their relationships to other materials in the solution and to the concentration of the whole solution, are factors which affect profoundly the growth of plants.

In a third paper[42] published jointly by Gile with C. N. Ageton, a discussion is given of soil experiments intended to test the validity of the lime-magnesia ratio hypothesis. The results were conflicting and the authors point out that the positive results as well as the negative results which they obtained, may have been due to changes in the reaction of the soil. To quote them further—"From effects of salts on plants grown in water cultures, we should not expect plants to be influenced by the ratio of the bases under the conditions obtaining in any but alkali soils." They point out—and this statement is well supported by numerous data from investigations on arid soils—that the latter may be very fertile and with a very wide divergence in ratios of lime to magnesia. They are therefore, at least to some extent, justified in attributing to the lime-magnesia ratio in the ordinary analysis of soils, decidedly minor significance, pointing out at the same time that in alkali soils such a ratio may be very important.

The same authors in a further communication[43] detail experiments with bush beans on soils containing varying quantities of

[41] Physiol. Res., vol. 1, no. 4, p. 133–244, May, 1914.

[42] Jour. Indus. and Eng. Chem., vol. 5, p. 33. Cited from E. S. R., vol. 28, p. 812, 1913.

[43] Jour. Indus. and Eng. Chem., vol. 5, p. 564. Cited from E. S. R., vol. 29, p. 520, 1913.

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lime and magnesia. They could not, however, in these experiments, detect any relation which was constant in soil and in plant between the amount of those two compounds in the soil and in the plants and in their effects on growth. To quote them again—"Bush beans appear to be independent of the lime-magnesia ratio in these soils and also of the increasing amounts of carbonate of lime. . . . Since the lime content of plants remained constant with increasing amounts of lime in the soil, it does not seem possible that this plant could have adapted itself to the conditions by precipitation of lime as oxalate." This, therefore, is in contradiction and reply to the claim made by Loew on that point.

Following these investigations, Meyer, whom we have quoted above, discusses[44] in general the lime and magnesia fertilizer question. Among other statements that author makes the claim, and gives evidence in support of his contention, based on his previous experiments, that the maximum yield of crops is independent of any fixed lime-magnesia ratio in soils.

In investigating the question of plant chlorosis in its relations with calcium carbonate, Maze, Rout and Lemoigne[45] found that corn remains green but that lupines and one species of vetch which was tested, become chlorotic in a medium containing an excess of calcium carbonate. A few drops (0.02%) of ferric nitrate restored the green color in a few hours. It is concluded from that that iron assimilation is prevented by calcium carbonate in accordance with the idea presented by Gile, the claim being made that calcium carbonate renders the iron insoluble. They further make the claim that the corn roots secrete malic acid which dissolves calcium carbonate and releases the iron. They believe that leguminous plants do not produce enough of this acid. The interest of this investigation in connection with our subject is that ill effects of an excess of lime may be overcome easily by means other than changing the lime-magne-

[44] Jahrb. Deut. Landw. Gesell., vol. 27, no. 3, p. 728, 1912. Cited from E. S. R., vol. 28, p. 820, 1913.

[45] Compt. Rend. Acad. Sci. Paris, vol. 155, p. 435, 1912. Cited from E. S. R., vol. 28, p. 425, 1913.

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sia ratio, indicating that certain balances between the salts in culture media are necessary, and that they may be necessary for widely different purposes and be brought about in widely different ways.

Following these investigations, Pisciotta[46] published results of analyses of sixty Italian soils. He showed that wide variations in the lime-magnesia ratio, due principally to a variation in lime content, obtained in these soils. In only one soil did he find the ratio equal to 1 and he found it less than 1 in four soils. When magnesium sulphate was applied to the soil at the rate of forty pounds per acre, the grain yield was increased if the application was made at time of seeding, and good net profits followed. When, however, the magnesium salts were added in the spring, the increase was small, or wanting. The best yields were obtained in soils with a high lime-magnesia ratio, but contrary to Loew's theory, profitable increases were also obtained in soils with a lime-magnesia ratio which was less than unity.

In making a study of cane soils, Hutin[47] found that cane was capable of accommodating itself to soils which vary in their lime-magnesia ratios so much that there might be from one and one-half to four times as much lime as magnesia in a soil without damage to the cane plant. The work was carried out on the coastal plain sugar cane soil of Peru. At least so far as the natural content of lime and magnesia in soils is concerned, this investigation would not seem to lend any support for the idea of the necessity of a certain ratio between the two materials.

In studies of a similar nature Russell[48] states that he has never noted cases in English soils which bear out Loew's claim of infertility in soils due to excess of magnesia in them. On page 144, of the same work, Russell points out that, in general, the ratios in English soils fall between 1 and 3 (CaO: MgO), but ratios of 4 and 5 are not uncommon, and in "chalk soils that may rise very

[46] Staz. Sper. Agr. Ital., vol. 46, 1913, no. 10, p. 643. Cited from E. S. R., vol. 30, p. 519, 1914.

[47] Bul. Assoc. Chem. Sucr. et Distill., vol. 31, 1913, no. 5, p. 347. Cited from E. S. R., vol. 30, p. 326, 1914.

[48] Soil Conditions and Plant Growth, p. 49, Longmans, Green and Company, 1912.

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high. No connection could be traced between the lime-magnesia ratio and the productiveness of the soil. Indeed table 58 shows that very good and very poor soils may have practically identical ratios." The table referred to gives analyses of the soils of England in question which make clear the relationships between lime and magnesia in them.

In further experimental work Haselhoff[49] has shown by a series of pot experiments with different crops that it was impossible to substantiate Loew's theory on the necessity for a definite ratio of lime to magnesia for every kind of crop. The results obtained in the growth of these plants were such as to give no opportunity for correlating the want or the presence of good plant development with the total quantities and ratios of lime and magnesia in soils tested in the pots.

Similarly Hopkins[50] describes a series of experiments in pots with wheat on the Marshall brown silt loam, one of the typical soils of Illinois. These experiments showed that magnesium carbonate was harmless to the wheat when added to the soil constantly up to 0.8%. In amounts exceeding that it suddenly became very toxic. In attempting to neutralize such toxic effects, additions of calcium sulphate were made in varying quantities to the harmful quantity of magnesium carbonate, but in the words of Hopkins "little support" was found for "Loew's ratio from these data."

In making a study of Indian soils with particular relation to acid conditions in them, Meggitt[51] carried out a series of experiments which resulted among other things, in the following statement by him: "The results of our experiments do not at all connect the value of lime with any such relationship," referring to Loew's lime-magnesia ratio. The work was carried out on an acid soil and plots in the field were used.

Of less emphasis, but of similar significance is the investiga-

[49] Landw. Jahrb., vol. 45, 1913, no. 4, p. 609. Cited from E. S. R., vol. 31, no. 1, p. 31, 1914.

[50] Soil Fertility and Permanent Agriculture, p. 170–172, Ginn and Company, 1910.

[51] Mem. Dept. Agr. India, vol. 3, no. 9, p. 240.

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tion of Miège and Compain,[52] bearing on the subject of magnesia in soils. They carried out field experiments with dolomite on plots about six-tenths of an acre in size. The dolomite had a lime-magnesia ratio of 1:5. The soil used was a clay loam containing 0.86% lime in the surface with no magnesia, and with 0.35% of each lime and magnesia in the subsoil. The applications of dolomite depressed the yields, while applications of lime increased the yields on these plots. This indicates that in the surface soil in which the application of dolomite should have been instrumental in making much better lime-magnesia ratios, since no magnesia was present at all to begin with, it really made conditions worse by making the ratio approach the one claimed by Loew to be ideal, and that an application of lime, which should have had the opposite effect because it increased that material in the total absence of magnesia, had the contrary effect of increasing the yields.

Believing at one time that the theory of Loew might account for the chlorotic conditions of citrus trees in certain parts of California in which large quantities of marl were found in the subsoil and sometimes also in the surface soil, Hilgard and Loughridge proceeded to inaugurate a series of investigations along two different lines, one of them aiming to overcome the bad effects of a high lime ratio as compared to magnesia by applying magnesium sulphate in large quantities, and the other by making a study of the lime-magnesia ratio in the soils on which chlorosis commonly occurred in that region. These investigations have never been published, but the writer of this review has referred to some of the results obtained, in an article[53] written some time ago. These results, in brief, have shown that magnesium sulphate applied in very large quantities and at different times, could not cure the chlorotic condition in the citrus trees in question. When on the other hand, the ratios of lime to magnesia in the soils were studied, it was found that good vigorous trees, showing no signs of chlorosis were found on soils with ratios of

[52] La Vie. Agr. et Rur., vol. 3, no. 19, p. 532. Cited from the Monthly Bul. of Agr. Intel. and International Inst. of Agr. at Rome.

[53] Pacific Rural Press, vol. 81, no. 24, p. 272.

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lime to magnesia which varied from 0.9: 1 to 3: 1, with many intermediary values, while ratios on soils in which chlorotic trees were found varied from 1.7: 1 to 4: 1. The worst tree encountered was found growing on a soil in which the ratio was 1: 1.7. This, it will be noted, is an intermediate value in the first group of ratios above referred to. These data, therefore, would lend but little support to the necessity of a certain lime-magnesia ratio for citrus trees. They do not of course exclude the possibility that, were the immediate cause of chlorosis removed, the lime and magnesia ratio as a factor in growth and production might come to the fore in a more important way, but at any rate, they furnish no evidence at the present time in support of such a view.

(To be concluded in May issue.)

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I. THE RED COLOUR OF THE MESOCARP OF SEEDED FRUITS IN THE PERSIMMON (*Diospyros Kaki*)

II. A VISUAL METHOD FOR ESTIMATING ASTRINGENCY

FRANCIS E. LLOYD

McGill University, Montreal, Canada

It has been pointed out by Mr. H. Harold Hume[1] that certain, though not all, species of the cultivated persimmon are characterized by the fact that, in the event that the fruit is pollinated, more or less of the mesocarp in the region of the developing seeds early takes on a reddish colour. This coloration had already been noticed to occur in fruits in those species whose fruit becomes non-astringent on the tree. This fact was communicated to me by Mr. George E. Roeding, of Fresno, California, in response to an inquiry proimpted by my suspicion[2] that the non-astringency in those fruits which become edible while still firm and attached to the tree, might be due to the oxidation of the tannin, a view which, as it eventuated, can not be supported in the light of all the facts. I had noticed furthermore that small masses of tissue containing the red colour commonly occur even in astringent fruits, that is to say, in those which lose their astringency only after artificially stimulated or after prolonged spontaneous ripening, following removal from the tree. The occurrence of seeds is therefore not a *conditio sine qua non* for the production of the colour, although, as Mr. Hume has said, it occurs regularly in the seeded fruits of certain kinds in such amount and constancy that the presence of the seeds may be suspected of having some connection with it. Further support for this conclusion came to my attention in 1911 and 1912. In

[1] A Kaki classification. Journal of Heredity, **5**: 400–406, 1914.

[2] Lloyd, F. E. The induction of non-astringency in persimmons at supranormal pressures of carbon dioxide. Science, 11. **37**: 228–232, February 7, 1913.

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1911 the fruits of two trees of *Taber 23*,[3] growing at Auburn, Alabama, became non-astringent only after treatment with CO_2, or prolonged keeping. The mesocarp was always clear opaque yellow, becoming watery on softening, though in these fruits, as in those of other kinds, an occasional spot of red colour might be seen. In September, 1912, however, it was found that all the fruits of these trees were non-astringent, and this condition was found not only in the fruits approaching ripeness, as indicated by their rich orange colour, but *in those still quite green* (Lloyd, *l. c.*). Mr. Hume, who examined these trees personally in 1914, informed me by letter (November 9, 1914) that the same condition then obtained, and held it to be connected with pollination and subsequent seed production.

Kindly responding to my ready willingness to look into the histological and cytological conditions obtaining in the tissues of these red-fleshed and non-astringent fruits, Mr. Hume provided me with a number of fruits of the race *Zengi*, which behave in the manner above adverted to. The results presently set down are based entirely upon these. Before proceeding to an examination of the seeded *Zengi* fruits, however, a brief review of the nature of the tannin-bearing cells in the persimmon will facilitate discussion.

These are large spindle-shaped cells found arranged in rather irregular, shorter or longer strands traversing the fruit in a longitudinal sense, exclusive of the endocarp from which they are absent. Each cell consists of a protoplast enclosing a very large central vacuole. The cell-wall is thin, as in the remaining parenchyma cells. The vacuole is filled with a mucilage-like emulsion colloid, a carbohydrate of the nature of cellulose[4] (here called *X*-cellulose), capable of indefinite solution in water until a late condition of ripeness of the fruit is attained, when it becomes coagulated, and later undergoes syneresis. As a result of its great

[3] "*Taber 129*" in my earlier papers on this general subject. There were but two trees of the race "Taber" at Auburn, and there was some uncertainty as to their identity. Mr. Hume designates them *Taber 23*.

[4] Clarke, E. D. Notes on the chemical nature of the "tannin masses" in the fruit of the persimmon. Biochem. Bull. **2**: 412–418, April, 1913.

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capacity for hydratation, any access of water to the tannin-cells, before coagulation is complete, causes the *X*-cellulose to swell sufficiently to burst the cell wall. After death of the cell, and when syneresis has advanced, the volume occupied by the *X*-cellulose is much less than previously, and its capacity for swelling is very limited and always insufficient to cause rupture of the cell wall.

Associated with the *X*-cellulose is the tannin. This, during the unripe stages, is loosely adsorbed by the *X*-cellulose so that upon hydratation of the latter sufficient to break through the cell wall, the tannin partly escapes into the surrounding water. As ripening becomes more advanced, the coagulation of the *X*-cellulose becomes more pronounced, and the adsorption of the tannin more complete. The amount which may then escape upon increased hydratation of the *X*-cellulose becomes less and less until it is too small to be appreciable. There is, of course, no such condition as complete non-astringency, cxcept in a merely gustatory sense, for tannin diffuses out of the even completely coagulated tannin-masses, but only very slowly. In this connection it may be pointed out that the earlier conception of "soluble" and "insoluble" tannin is inadequate. The fruit is then non-astringent. If the fruit is kept for some time, the tannin becomes oxidized and red in colour when the tannin-masses (the masses of coagulated *X*-cellulose and adsorbed tannin) can be readily recognized. Syneresis, too, becomes pronounced.

Meanwhile, the hydrolysis of the intercellular substances has proceeded, together with changes in the content of sugar and other substances,[5] in part consequence of which the fruit becomes softened, even, at length, to wateriness. The tannin cells are then quite free from each other and from their neighbouring parenchyma cells, and these, *inter se*, equally so. The various changes do not, however, proceed in all fruits at the same relative rates, for some fruits become non-astringent before softening, others only after an advanced stage of softening has been reached.

[5] Bigelow, Gore and Howard. Journ. Amer. Chem. Soc., **28**: 688, 1906.

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This discrepancy in the rate of ripening may be much more pronounced as between particular cells. For some reason not understood, but obviously connected with the early death of the cells involved, the change of the X-cellulose from the uncoagulated to the coagulated condition is compassed in a greater or smaller number of tannin cells early in the development of the fruit. These cells then die, and the adsorbed tannin becomes oxidized. Such cells may be recognized by the form and colour of their tannin masses, which are red and show marked syneresis.

The occurrence of considerable numbers of such red tannin masses within a restricted volume of tissue gives it the red appearance identical with that noted in seeded fruits, and at the same time a "gritty consistency,"[6] for the individual tannin masses are rather hard and quite insoluble in water.

This then is the normal course of that change among the several constituting ripening which produces a non-astringent from an astringent seedless fruit. It is identical with the corresponding change in the date, banana, sapodilla, etc.

The purpose of this paper is to show that the changes in seeded fruits are to be regarded as identical. The examples of *Zengi* fruits supplied by Mr. Hume were peculiarly suited to decide the question, as only the region of the pericarp adjacent to a seed was non-astringent, the bulk of the remainder being normally and extremely astringent. The accompanying diagram (fig. 1) enables us to define particular areas in a transverse section of a fruit in which there was only one seed. Surrounding the seeded locule and embracing also the two adjacent ones was a mass of red tissue. At the time of first examination the flesh was firm throughout the fruit, light yellow in colour, and opaque, the opacity being due to the air in the intercellular spaces. At one place there was a bruise.

The red coloured region (fig. 1, *a*) was entirely non-astringent, but had in every respect a normal structure, save that a considerable number of the tannin-masses were shrunken and red. The remainder, however, were colourless, in an early condition

[6] Hume, H. H. Effect of pollination on the fruit of Diospyros Kaki. Proc. Soc. Hort. Sci., Florida, 1913. 88–93, March, 1914.

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of syneresis, and betrayed nothing different from the tannin-masses of a non-seeded fruit when just arrived at the point of non-astringency.

The region *b* was quite free of coloured tannin-masses, but *was also non-astringent.* The tannin-masses were in a similar condition to those of the uncoloured ones in region *a*, showing incipient syneresis. The absence of astringency was determined by tasting (by two persons) and by the tests fully described by myself elsewhere.[7]

The regions *c* and *c* were slightly astringent but the more so the nearer the limits between region *c* and region *d*. The tannin-

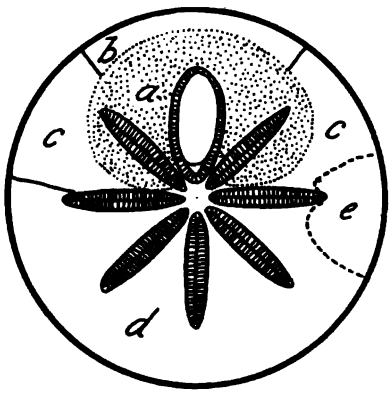

Fig. 1.

masses were in an early stage of coagulation. The tannin could diffuse slowly out of the *X*-cellulose and precipitation membranes consequently formed, but equally slowly. The power of hydratation was still sufficient to enable the now jelly-like *X*-cellulose to burst the cell wall in many instances, and the usual precipitation membranes would then be formed. Under such conditions as-

[7] Lloyd, F. E. The behavior of tannin in persimmons, with some notes on ripening. Plant World **14**: 1–14, 1911.

The tannin-colloid complexes in the fruit of the persimmon. Diospyros, Biochem. Bull. **1**: 7–41, 1911.

Ueber den Zusammenhang, *u. s. w.* Zeitschr. f. Chem. u. Ind. d. Koll. **9**: 65–73, 1911.

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tringency to the taste is markedly developed in the course of a minute or so, the first impression being of entire non-astringency.

Region *d* was completely and promptly astringent. The *X*-cellulose was in an entirely uncoagulated condition, and when escaping from cells whose walls were broken, did so in a gushing stream, due to its great hydratation and unlimited solubility. The diffusion of tannin was correspondingly prompt and extensive. If temporary syneresis was induced in the outer zone of the tannin mass by means of a suitable reagent (alcohol, *e.g.*), the internal pressure would cause the reduction of free inner surfaces so that the canals[8] would be broken into a series of globular spaces, thus demonstrating the soft and yielding character of the *X*-cellulose, an emulsion colloid.

In the region of the bruise (*e* in the figure) the tissues were soft and watery, the intercellular spaces were partly filled with the *X*-cellulose extruded from broken tannin cells by the pressures which caused the bruise, and extra-cellular precipitation membranes had occurred, while some tannin-masses showed complete syneresis. While the tissues were still astringent the change toward non-astringency has proceeded at different rates in the various elements.

It will be seen from the foregoing that the *region of non-astringency is not coextensive with that of the red-coloured tissues*, from which the obvious inference may be drawn that the red coloration is a consequence of changes leading to non-astringency and itself not the cause of it. The condition of coagulation of the *X*-cellulose content of the tannin-masses, if not indeed the death of the tannin-cell, is a condition antecedent to that when oxidation of the tannin occurs, so that the non-astringency of seeded fruits is the result of the same changes which occur in non-seeded fruits, but induced at an earlier stage of development.

The early death of a certain proportion of the tannin cells is responsible for at least one other disturbance in the usual sequence of events. The softening of the fruit is due, as is well known, to the hydrolysis of the intercellular pectose bodies. It

[8] Lloyd, F. E. *l. c.*

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has further become clear to me from my studies of changes in ripening fruits (and of analogous changes in other parts) that the hydrolysis of the interwalls (usually regarded as middle lamellae or primary membranes) depends on the secretion of appropriate enzymes by each particular cell, and indeed by each particular contingent region of the protoplast. In consequence, two adjacent cells may be set free of all other surrounding cells, but themselves remain attached to each other. The softening and the deliquescence of the persimmon fruit may be prevented by killing the tissues just as may, also, the process leading to non-astringency[9] so that the early death of any of the component cells of the mesocarp for any cause, spontaneous or otherwise, should lead to the same result coextensively with the cells or tissues involved. This, in point of fact, actually occurs in the red-coloured parts of seeded fruits. Not only do the red tannin cells themselves remain attached to each other, for many days after the fruit is completely non-astringent, but the adjacent parenchyma cells also remain attached to them, while the uncoloured tannin cells become separate from each other (but not from adjacent red tannin cells) and from the parenchyma cells. To prove this it is necessary only to shake up portions of overripe mesocarp in water, when the cells will either fall apart or cling together in accord with the conditions just described.

There remains the question as to the reason why the presence of seeds should influence the rate of the process of becoming non-astringent and the consequent death of many tannin-cells, together with the resulting reddening by oxidation of their tannin. Any answer must however be of a general enough nature to include the fact that the same result occurs, although less extensively, yet independently of seed production, and the further fact that the occurrence of seeds in certain varieties does not induce the changes described. We have also the observation that, in the variety *Taber 23*, the entire fruit had become non-astringent even while still green (at Auburn, Alabama, in 1912). Whatever the answer, the fact to be accounted for is the abnor-

[9] Vinson, A. E. The stimulation of premature ripening by chemical means. Journ. Amer. Chem. Soc., **32**: 208, February, 1910.

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mal hastening of a single process, namely the coagulation of the emulsion colloid with which the tannin is associated. I have shown that carbon dioxide in major dosage may do this. A sufficiently rapid accumulation of this gas in the tissues, either locally or generally, is quite thinkable and would readily suggest itself as the explanation of the changes in the region of a large growing seed, such as that of the persimmon, but unfortunately this view does not accord with all the facts. It is, however, at the moment the only plausible theory, and any other that might be offered would harmonize still less with our present knowledge of fact.

II. A VISUAL METHOD FOR ESTIMATING ASTRINGENCY

(A Preliminary Note)

The following method is based on the observation that the degree of astringency depends on the degree of adsorption of the tannin by the *X*-cellulose. Since this increases during ripening, the amount of tannin which can be adsorbed by another substance decreases. The other substance, according to previous experience, is that of the mucous membranes. If, however, a suitable adsorbing agent (*e.g.* pure cellulose in the form of filter paper) be substituted for the mucous membranes, a partition of the tannin will occur, the amount being taken up by the filter paper being directly proportional to the astringency. The procedure is as follows:

Slightly moistened filter paper is laid on a cut surface of the fruits to be examined, and allowed to remain for a given length of time. Upon removal a tannin reagent giving a colour reaction is applied and therewith an image is developed. The strength of the image (which appears as a contact print of the tannin-tissues) will be great or small according to the amount of tannin adsorbed. The results which have been obtained enable one to determine astringency and non-astringency quite as accurately as, and much more comfortably than, by tasting.

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BOOKS AND CURRENT LITERATURE

A Criterion of Physiological Vigor.—A recent contribution by Benedict[1] presents what appears to be conclusive evidence of progressive senile changes in the leaves of *Vitis vulpina* and suggests a new criterion by which different plants may be compared with regard to physiological vigor. The paper opens with a comprehensive review of the present status of our knowledge of senility in both animals and plants. This section is followed by a report of the author's own studies, and this is followed, in turn, by a section devoted to theoretical discussion.

If a leaf is examined by transmitted light (a photographically enlarged print is actually used), it is seen that the organ is composed of anastomosing veins and intervenal masses of tissue, which Benedict terms vein islets. These islets may be counted and their average area in the plane of the leaf may be determined. It is found that leaves of young plants of *Vitis vulpina* are characterized by the possession of large intervenal areas, while leaves of old plants have much smaller areas. For plants 3 to 5 years old the average area of the vein islets was found to be 0.4941 sq. mm.; for plants 6 to 11 years old, 0.3727 sq. mm.; for plants 14 to 25 years old, 0.2969 sq. mm.; for plants 28 to 35 years old, 0.2211 sq. mm.; and for plants 50 to 70 years old, 0.1638 sq. mm. With increasing age of the plant the decrease in the size of the intervenal areas is first very rapid and then slow, but it still decreases between ages of 60 and 70 years and no evidence is presented to favor the supposition that a constant size is attained with great age, though this might be expected. At any rate, plants much older than 70 years must be studied if a limit of this decrease is to be discovered. Here, then, is a simple means by which the age of this plant may be approximately determined, without cutting the stem.

Of course the intervenal areas increase in size with the development of the individual leaf, but the range in size is found to be related to the age of the plant. Thus the various stages of leaf development for a vine 25 years old showed a range of islet area of from 0.010 to 0.190 sq. mm.,

[1] Benedict, H. M., Senile changes in leaves of *Vitis vulpina* L. and certain other plants. Cornell Univ. Agric. Exp. Sta. Memoirs 7: 281–370, 1915.

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while the corresponding range for a plant only 10 years old was from 0.015 to 0.260 sq. mm. While external conditions during leaf development do influence the size of the vein islets, this effect appears to be superimposed on the more pronounced influence exerted by internal conditions, so that if the young and old plants grow with the same environmental complex the age difference is still clear.

For quick estimation is it sufficient to count the number of veins intersected by a line drawn across the leaf. The count is made for a line 2 cm. long. It is obvious that, the smaller the islets, the larger is the number of veins this intersected.

Evidence pointing in the same direction is presented for a number of other plants, such as *Vitis bicolor* Le Conte, *Tecoma radicans* L., *Salix nigra* Marsh, *Castanea dentata* Borkh., *Quercus alba*, L., etc. It was found that the leaves borne out by sprouts coming from the stump of a tree show intervenal areas of the size characteristic of the age of the stump.

In the case of cultivated plants propagated by cuttings the size of the islets is related to the number of years that have elapsed since the last reproduction by seed. Thus a Concord grape vine, propagated by cuttings for 70 years bore leaves with 66 veins per 2 cm., while the leaves of a Concord seedling 7 years old showed only 35 veins per 2 cm. Similarly, a Hubbardston apple seedling 15 years old bore leaves with 30 veins per 2 cm. and the corresponding number of veins for a Hubbardston apple propagated by grafts for 82 years was 45. It thus makes no difference whether the plant is propagated by cuttings or whether the original stock is alone considered, the results are practically the same. Even after grafting the scion appears (by this criterion) to be as old as the stock from which it was derived. Physiological age is thus to be measured, in this connection, from the last propagation by seed.

Approximate determinations show that various other leaf characters vary in a direction parallel to that shown by the variation in size of vein islets. Thus, leaves of a vine with 6 growth rings gained 12.7% of their green weight in a day, while the corresponding gain of leaves of a vine having 20 rings was only 2.1%. The respiratory rate (CO_2 elimination) also falls with increase in area of vein islets. Vines averaging 7.3 years old, bore leaves that eliminated CO_2 amounting to 0.0349% of green weight per hour, while this rate for vines averaging 25.4 years old eliminated 0.0297% per hour. If the leaves are dried and powdered the powder from old plants has a much lower imbibing

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power for water than that from young plants, and the leaf powder from young plants is markedly more acid than that from old plants. Stomatal frequency is much greater for leaves of old plants than for those of young ones, but the average length of stomatal opening is greater for young plants. The average length of palisade cells was found to be 12.2 micra for vines with 5 rings, and 10.3 micra for vines with 20 rings. Finally, some evidence is presented suggesting that the volume ratio of cytoplasm to nucleus in leaf cells is greater for young than for old plants.

In many respects, therefore, plant senility alterations appear to parallel the corresponding changes recorded for animals, and it is once again indicated that plants and animals are essentially alike in their general protoplasmic characters. The physico-chemical explanation of senile change is not yet apparent, however. Benedict emphasizes a decreased permeability of the protoplasm of cells of old plants, as a possible cause of age alteration.

To the reviewer, the criterion of size of intervenal areas appears to promise much in connection with the comparison of different plants as related to their surroundings. The possible influence of environmental conditions on vein islet size in the same plant form should receive attention, and different forms should be compared by this criterion.—B. E. Livingston.

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NOTES AND COMMENT

The first volume of the Proceedings of the National Academy of Sciences (1915) contained the following papers of botanical interest: Phoradendron, by William Trelease; The Morphology and Relationships of *Podomitrium malaccense*, by Douglas H. Campbell; A Phylogenetic Study of Cycads, by Charles J. Chamberlain; A Method of Prophesying the Life Duration of Seeds, by William Crocker and J. F. Groves. We mention these papers merely to help a little bit in bringing them out of the concealment which their place of publication has afforded them. In these days of great scientific activity and numerous journals it is difficult for a specialist to keep track of all the papers in his subject, even so far as they are to be found in the journals confined to his own subject. The proceedings and transactions of academies and societies, whether local or national, and other publications of mixed contents, add even greater difficulty to the following of current literature. Every worker who has endeavored to consult all of the writing on a given subject finds himself, as he nears the completion of his task, with a few unfound references to papers in obscure or expensive publications with miscellaneous contents. It matters little whether the publication is obscure or expensive, for in either case it is likely to be absent from his nearest libraries. Some of the journals which cover the entire field of science have devoted themselves to general papers and addresses; others have given their space to piquant but unsatisfying reports of progress, or to preliminary promises, many of which are never fulfilled. It is to be hoped that all proceedings and transactions of an omniscientific character will rapidly enter one or the other of these classes so that they may be comfortably forgotten.

At the close of the present academic year the University of Chicago will hold elaborate exercises in celebration of its Quarter Centennial. Each of the departments will invite its graduates to be present at specially arranged programmes and dinners. The celebration which has been planned by the members of the Botanical Department will commence on June 2 and last for five days. Addresses will be delivered by four graduates of that department: Prof. T. C. Frye, of the Univer-

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sity of Washington; Prof. B. E. Livingston, of The Johns Hopkins University; Prof. George H. Shull, of Princeton University; and Prof. F. L. Stevens, of the University of Illinois. The great service which the University of Chicago has rendered in the development of American botany is eloquently attested by the number of doctorates which have been conferred in this subject. The first was granted in 1897, and the degrees of the present year will bring the total to seventy-nine.

In the November issue of THE PLANT WORLD announcement was made regarding prizes which are offered for the best contributions in soil physics. Three well known pedologists have consented to act as judges of the papers which are entered in this competition. They are Mr. R. O. E. Davis, in charge of Physical Investigations in the Bureau of Soils; Prof. A. G. McCall, head of the Department of Agronomy in Ohio State University; and Prof. Charles F. Shaw, head of the Division of Soil Technology in the College of Agriculture of the University of California. Competing papers should be in the hands of the Editor on or before December 1, 1916.

Mr. George B. Sudworth has published the second of his series of bulletins on the trees of the Rocky Mountain region, covering the spruces and balsam firs. The descriptive matter is accompanied by 25 plates and 10 distribution maps (Agricultural Department Bulletin 327).

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A CRITIQUE OF THE HYPOTHESIS OF THE LIME-MAGNESIA RATIO

CHARLES B. LIPMAN

University of California, Berkeley, Cal.

II

THE INDIFFERENT INVESTIGATIONS OR THOSE OF NEITHER POSITIVE NOR NEGATIVE SIGNIFICANCE ON THE QUESTION OF THE LIME-MAGNESIA RATIO

Numerous experiments have been carried out by many investigators which deal as do some of Loew's earlier investigations, more specifically with the functions of lime and magnesia independently in plant growth, and also with such matters as the relationship of lime and magnesia, each alone to other nutrients in the medium in which the plant is grown. Some of these may have direct bearings on the lime-magnesia ratio, but not as clearly as those which are above reviewed. For that reason, a number of the typical ones, and perhaps most of them which are of interest, are here briefly reviewed for use by those who are interested in the question.

T. H. Kearney and F. K. Cameron[54] made a study of the effect of certain components of alkali soils upon seedling plants. Their results, dealing principally with culture solutions, made it quire clear that calcium and magnesium could antagonize each other, and further that they could each antagonize toxic effects of other salts.

Ulbricht, in 1894, carried out some investigations which were published in two papers. The first[55] dealt with a study of the action of lime and magnesia in marl and burnt lime. Ulbricht applied 710 pounds per acre of burnt lime which was poor in

[54] U. S. D. A. Rpt., no. 71, p. 7–60, 1902.

[55] Chem. Centb. 1894, vol. 2, p. 803. Cited from E. S. R., vol. 6, p. 628, 1894–5.

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magnesia, and he found that it delayed markedly the ripening of oats. A similar application of the so-called "gray" lime gave much less marked results. The difference in the action of these two forms of lime is ascribed by Ulbricht to the magnesia which is found in the gray lime. He found further that caustic magnesia (burnt magnesite), as well as magnesium carbonate, were highly injurious to oats. Moreover, he found that the injurious effects of such magnesia applications were not always prevented by the simultaneous applications of caustic lime or of calcium carbonate. He found that barley was more resistant to the injurious action of magnesia than oats.

In the second paper,[56] the same author studied the relationship of lime applications to the yellow lupine and to other plants. He found that the yellow lupines were injured by lime and that the latter was particularly injurious when it contained 40% of magnesia. The magnesia was found by him to be especially poisonous, and he found it besides poisonous not only to lupines, but to barley, vetch, and radishes. The effects of the application of magnesia extended over at least two years, when radishes followed the lupines on the same land.

In investigations carried out about the same time by Schreiber,[57] two complete fertilizers were tested. The first contained $CaH_3(PO_4)_2$ plus calcium sulphate and magnesium carbonate. The second contained phosphate of soda with magnesium carbonate and calcium carbonate. The experiments were made with oats and turnips on sandy, humus, and loam soils, and the fertilizers were applied to the first crop only. In every case the yield was much lowered with the second fertilizer above described, and Schreiber claims that this is due to the fact that the action of the carbonates of lime and magnesium in making phosphoric acid insoluble renders difficult the proper nutrition of the plant. The differences were noted to be more marked in the case of turnips because, in Schreiber's opinion, the retrograde action had become more complete.

[56] Landw. vers. Stat., vol. 52, p. 383.

[57] Rev. Agron. Lowain, vol. 4, p. 66. Cited from E. S. R., vol. 7, p. 104, 1895–6.

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Loew and Honda,[58] in making a study of the lime and magnesia requirements of conifer trees, tested *Cryptomeria japonica, Thuja obtusa* and *Pinus densiflora*. Lime is considered, as a result of these experiments, to be best for such trees, while magnesian soils are relatively poor for them. The intrinsic value of lime in the soil for these plants is claimed to be shown even when it is much surpassed in quantity by the magnesia. The lime in the soil manifests its presence by the production of greatly shortened leaves.

Soon after the appearance of this work there was published by R. Heinrich[59] an essay on marl and marling which received a prize. Of immediate interest to us in this paper is one fact mentioned by Heinrich, namely, that of a series of substances tried on lupines, magnesium carbonate proved the most injurious in that 0.5% of magnesium carbonate completely checked the growth of plants.

Likewise Passerini[60] found that magnesium carbonate, applied at the rate of two to five hundred kilograms per hectar reduced the yield of wheat and injured its quality.

Bearing more directly on the question of the action of different compounds of calcium and magnesium on plants D. Meyer[61] carried out a series of experiments in pots of 6,000 grams capacity. Sand and peat and sand loess were used in these pots. Oats, potatoes, horse beans, vetch, and a mixture of plants like grass and alfalfa were the plants tested. Calcium was used in the form of calcium sulphate, calcium carbonate, and tri-calcic phosphate, while the magnesium was used in the form of the carbonate. The calcium and magnesium were all employed in various combinations with each other and with potash and nitrogen. As a result of these investigations it was found that gypsum depressed the yield in the grass and alfalfa mixture. With larger applications the reduction in yield was found to be proportionate

[58] Bul. Col. Agr. Tokyo, Japan, vol. 2, p. 378. Cited from E. S. R., vol. 7, p. 869, 1895–6.

[59] Paul Parey, Berlin, 1896. Cited from E. S. R., vol. 8, p. 969, 1896–7.

[60] Bol. Scuola. Agr., vol. 3, p. 140. Cited from E. S. R., vol. 9, p. 749, 1897–8.

[61] Landw. Jahrb., vol. 31, p. 619.

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to the application. Potatoes were not thus affected, but on the contrary, calcium sulphate and calcium carbonate acted alike for that crop. The injurious effects of gypsum were overcome by applications of either calcium or magnesium carbonate along with it. Its effects were also reduced by mixing loam with sand. When used in small amounts, but only then, magnesia increased the yield of grass and alfalfa; larger applications reduced the yield in the case of that crop mixture. On the other hand, in the case of horse beans and vetch, the yield was not reduced by the application of magnesia. In general, it appeared that the magnesium carbonate was apparently capable of almost completely replacing lime in spite of the fact that the highest yields were always obtained when calcium and magnesium carbonates were used together.

In the continuation of his investigations above discussed on the effect of liming in growing crops, Ulbricht[62] carried out another series of pot experiments with barley. He found in these that lime "fertilizers" increased markedly the yield of barley in all amounts used. The weight of the grain in every case was reduced by the application of lime and marl in February. The tillering of the grain was invariably increased by lime and magnesia. A heavy lime application plus a heavy magnesia application increased all phases of the growth of plants, but the straw more particularly than the grain, and the weight of the grain was less. Heavy applications of magnesian lime reduced the yield of grain and straw.

Of a much more indirect nature is the investigation of R. Averna-Sacca[63] on the chlorosis of oranges and other plants on ferruginous soils. Soil analyses and pot experiments were carried out in an attempt, by various means, to cure grape vines, coffee plants, orange trees, etc., of chlorosis. A large number of remedies were employed and as a result Averna-Sacca concludes that chlorosis is due principally to a deficiency of magnesium and

[62] Landw. vers. Stat., vol. 57, p. 103.

[63] Bol. Agr. (Las Paulo) 13th Ser. 1914, no. 2, p. 129. Cited from E. S. R., vol. 28, p. 153, 1913.

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not to a deficiency of iron, as claimed by other investigators above cited, and that magnesium carbonate when applied to the roots, in solution, gives good results.

CRITICAL REMARKS ON THE INVESTIGATIONS ABOVE REVIEWED

In a critical examination of the foregoing data which are in support of Loew's lime-magnesia ratio hypothesis, one can not help being impressed with the oversight, or at least lack of attention to several important factors which enter into a consideration of the validity of the hypothesis in question. The lack of extensive field experiments, the very short period allowed in the different experiments for testing the hypothesis, the addition of calcium and magnesium salts in various forms to media, whether they be soils, sands, or solutions of widely different character and composition, as well as an utter disregard of the general principle of antagonism between salts, or antagonism between ions, which is coming to be more and more firmly established every year, would all seem to call in question the desirability of the acceptance of the results discussed as adequate in themselves at least, for the establishment of Loew's hypothesis.

We may now proceed to a more extended examination of the investigations which are above reviewed. In examining the data submitted in favor of the lime-magnesia ratio or those above referred to as the positive investigations, we find that the chief aim has been to overcome an excess of either lime or magnesia in a soil by the addition of the other, regardless of whether the lime or magnesia was added in an artificially prepared soil, or was present to begin with in a natural soil. After such additions have been made and the crops grown, then, depending upon the effects which additions of materials like those named produced on the crop, certain deductions were drawn as to the suitability of one or another ratio for the particular crop under investigation. The criterion, then, for the establishment of the principle of the lime-magnesia ratio hypothesis as well as for the establishment of the proper ratio with the principle for a given crop, is merely the kind of growth obtained by a certain chemi-

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cal treatment of the medium in which the plant is produced. To one who has given careful thought to the rôle of chemical elements and compounds in plant growth, this kind of experiment with the object in view adopted, together with the mode of drawing conclusions, appear, to put it mildly, to be somewhat unusual in the realm of scientific work. Admitting, to begin with, that magnesium is toxic to plants when found in the medium of growth beyond a certain relatively small concentration in soluble form (and no one will deny that who has ever made experiments with magnesium salts) in plant growth, why should it be assumed that when to such toxic quantities of magnesium certain quantities of calcium are added and the toxic effect is wholly or partly overcome, that it is because the lime-magnesia ratio has been brought to the optimum in that particular medium? Why may it not be assumed, for example, when soils are employed, that the addition of the calcium salt has influenced more markedly the decomposition of the nitrogenous fraction of the organic matter, and therefore placed at the disposal of the plant more available nitrogen; or that through the whole principle of the substitution of bases or exchange of bases, potassium in necessary quantities, may have been set free from its insoluble combinations by the calcium; or that phosphoric acid, which is present in the soil in the more insoluble aluminum and iron phosphates, may have been rendered more soluble by its combination in part with the calcium? Or, if we may be allowed to surmise still further, it is not at all improbable that the addition of calcium which we know to be, among the alkalies and alkali earths, the most active precipitant of clay and binding material for sand, produces marked physical changes which would bring about the improvement which is noted as the end result of the application of calcium. Indeed it is evident at the present time in plant physiological investigation that a certain beneficial effect induced by a certain kind of treatment may wholly mask, through its marked good effects, the bad effects of say, a toxic material, and it is not at all impossible that calcium may thus bring about better conditions when added to a medium containing magnesium salts in toxic quantity.

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To add to all these possibilities of quite different effects of an addition of calcium or magnesium one to the other, when either one is present in toxic quantity, we may still further consider that in some of the investigations above reviewed it was found that that not only the addition of calcium to magnesium or magnesium to calcium, but an addition of another material like potassium nitrate, might very much improve the action of the antagonistic element of the two which we are considering, and a great amount of evidence has been adduced from past experiments on balanced solutions in plant growth which indicates quite clearly that many elements can be used as antagonistic agents to many others. Why not, therefore, merely regard the calcium as an antagonistic agent to magnesium without involving the necessity of a definite ratio between calcium and magnesium as being a necessary condition for the successful growth of plants?

The positive investigations further, despite their rather large number, are by no means fully convincing in their evidence that certain definite ratios of lime to magnesia are necessary for the proper growth of plants because these ratios are found to vary so much. In some instances, we have ratios varying from 1:1 to 1:2, to 1:3, for the same plants, whereas in others, we have ratios which vary from 1:1 to 6.7:1 as in Konovalov's experiments, for example. Then again, we have a wide variation in ratios for different plants, some of them evidently requiring much higher ratios of lime to magnesia than others. Considering the wide diversity in soils upon which plants are grown and the wide diversity in lime and magnesia contents and ratios in those soils in all parts of the world, and that factors quite outside of the calcium-magnesium ratio in question must be taken into account, is it at all likely that the lime-magnesia ratio exercises so potent an influence on the welfare of plants in soils as Loew and his followers would have us believe?

In following the subject further, let us consider for a moment the negative investigations. Here we find strikingly enough, just as many investigations which cast doubt, and serious doubt, on the necessity of certain definite ratios of lime to magnesia for plants as those which favor the idea of the necessity for such a

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ratio. It will be noted, moreover, in the table which is specially drawn up and presented herewith to compare the number of positive and negative investigations, that in the latter case, the experimenters are drawn from a much wider range of territory and must have worked under conditions which made them quite independent of influencing one another. Not only their media, but their plant materials, were of a large variety, giving but little opportunity for a convergence of opinion, due to such causes, as might operate in the case of the investigators supporting the positive side of the question. The negative investigations further insofar as they deal with many of the same plants and many of the same chemical compounds that were included in the positive investigations, and yet resulted in negative results, would seem to cast still further doubt on the validity of Loew's lime-magnesia ratio hypothesis.

The investigations placed under the head of indifferent investigations are such as to render perhaps more clear the function of the specific elements, calcium and magnesium and to aid us in forming a proper critical opinion, or in taking a properly critical attitude with reference to the positive and the negative investigations. In showing the peculiarity of action of specific elements they make very clear, for example, the great variation in physiological action under different circumstances of magnesium and calcium. This is nowhere better exemplified than in Voelcker's experiments which show the beneficial effects of lime and the harmlessness of lime in very large quantity, and on the other hand, the distinctly harmful nature of magnesium to plant growth.

GENERAL CRITICAL REMARKS

Many of the statements above reviewed as being unfavorable to Loew's lime-magnesia ratio hypothesis have been answered by Loew. For example, mention is made above of Loew's objection to Gössel's data because Gössel used secondary potassium phosphate, while Loew used primary potassium phosphate. Loew makes the claim that the former reduces the injurious effects of an excess of magnesium. Admitting that it does, it is

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the very best kind of an argument for the introduction into the lime-magnesia ratio problem of other factors which are quite different from the antagonism between calcium and magnesium (which no one will deny exists) that may regulate the growth and even affect it, seriously, of the plants under consideration, without regard to any specific ratio between lime and magnesia.

Likewise, Loew's objection to Meyer's investigation is one that is hardly tenable because the number of plants used per pot and the time of harvest to which Loew objects, are sources of error, the like of which might be found in other aspects of pot or water culture experiments carried out by Loew, or anybody else. So, also we may cite Loew's objections to Gile's investigations on the basis that plants were used which were lime-loving plants and that therefore they were not affected by excessive quantities of lime, and hence the lime-magnesia ratio became a question of minor importance with such plants. But Gile continued his work with other plants, such as rice and bush beans, which were differently affected by lime, since they were not known to produce acids equivalent to the citric acid of say, the citrus tree, for precipitating the calcium, and yet no evidence was found that a relationship existed between the growth and welfare of the beans and rice and the ratio between lime and magnesia in the soil, or in other media employed.

Studying the subject generally, one is constrained to wonder why we should seek so far fetched an explanation of the antagonistic effects of calcium to magnesium and vice versa, so far as they exist, when we have the general principle of antagonism between ions as one of much firmer establishment by reason of a much wider test and one which in the light of all that we know in plant physiology and in chemistry, is accompanied by much greater cogency and rationality. That the toxic effect of an excess of magnesium salts can be neutralized by other materials than calcium we have ample evidence in the investigations of many plant physiologists, among them Osterhout, McCool, Miyake, the writer, and others working in a less elaborate way on that subject. So, too, we have ample evidence on the antagonistic influence of many other salts to calcium when calcium is present in form or quantity of a character to be toxic.

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The reviewer here purposely omits lengthy consideration of the microorganisms which have been dealt with from similar standpoints, giving primary consideration to the higher plants themselves with regard to the lime-magnesia ratio. He has done so because of Loew's objection to one of his early publications which attested to the lack of antagonism between calcium and magnesium for *Bacillus subtilis* on the basis that the fungi and bacteria are not affected by a lack of calcium since nucleo-proteids and their importance in the chlorophyll bearing parts of the higher plants probably have no analogy in the realm of the protista, and also because effects on the microorganisms are not necessarily translatable into terms of significance for the higher plants. Nevertheless, it may be mentioned in passing that in investigations carried out in the writer's laboratory, Kelley has shown that no antagonism obtains between calcium and magnesium carbonates so far as ammonifying and nitrifying flora of certain soils are concerned. In further investigations the same experimenter has pointed out that though all soils do not act similarly to the California soils and that the relationships in effects between calcium and magnesium carbonates may often reverse themselves, that nevertheless, despite all of that, little reliable support could be found for the existence of a definite lime-magnesia ratio for the soil flora.

On the side of the higher plants, however, the writer has also had occasion to carry out experiments on the lime-magnesia ratio which remain as yet unpublished. These experiments were carried out with beans and with citrus seedlings in the greenhouse, in pots containing good, fertile soil. In the case of the beans, no evidence through various mixtures of calcium and magnesium carbonates could be obtained of the existence of a definite optimum ratio of lime to magnesia for those plants. Always, there was present the marked toxicity of magnesium carbonate; likewise always a lack of evidence of the toxicity of calcium carbonate, and no unexceptionable evidence indicating points at which these were found in proper ratios for the crop in question. But the experiments with beans lasting only two years should not be perhaps over-emphasized for such purposes, and it is possible that

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a longer time given to these experiments might show something more, despite the fact that they are in accord with the negative investigations above reviewed. It should be remarked here, however, that in the citrus tree experiment which has now been carried on for over three years, the only evidence that we could obtain was that magnesium carbonate was extremely toxic to citrus trees and that at a toxic quantity of magnesium carbonate of 2% to begin with, additions of lime carbonate in all quantities up to 10% with intervals of 1%, were powerless to mask in anywise the toxicity of magnesium carbonate. Even 1% magnesium carbonate was found to be distinctly toxic to the citrus seedlings, whereas on the other hand calcium carbonate up to 10% of the dry weight of the soil, added to a lime content of 1.5% already in the soil, had no detrimental effect whatsoever. There was a difference in the shape of tree produced, as affected by lime treatment, the soils with the highest lime content giving a shorter tree growth, with more abundant foliage, and the soils with the smaller lime content, a taller tree growth with sparser foliage. Throughout the three years, however, only a thrifty condition has been observed in the trees treated with lime only, and nothing more, as judged by the green color of the leaves and the generally vigorous appearance of the plants. We have further found that though we could not overcome the toxic effect of the very toxic magnesium carbonate for the citrus trees, that when the magnesium carbonate was allowed to remain in the soil for a year and a half or two, and the soil remained uncropped, that after that citrus trees could be grown, but the growth made is always very slow and unsatisfactory.

There should not be omitted from our consideration here the work of Hansteen[64] on the relationships of certain salts of the soil to plants grown in solution cultures. While Hansteen seems to accept the general idea of Loew with reference to the lime-magnesia ratio for purposes of farm practice, he nevertheless points out certain objections to the theory even when regarded from the viewpoint of the physiological action of calcium and magnesium respectively which are above discussed. Thus, for ex-

[64] Jahrb. fur Wissen. Bot., vol. 47, 1909–10, p. 289.

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ample, it is noticed that in wheat plants grown in solutions which are rich in magnesium, or even in potassium, the color of leaves is always a dark green, whereas in the calcium-rich solutions, it is a yellowish green. A similar thing has also been noticed by the reviewer in bean plants treated with an excess of magnesia and lime. Hansteen points out that the damage done to plants in calcium-free solutions consists in the great swelling of the cells of the roots to the point of final bursting and disintegration, making a soft spongy mass of the feeding roots. Here we have, therefore, another example merely of the essential nature of calcium to plant growth, showing perhaps different phases of the manner of its functioning in plant life, but no evidence of the necessity of certain ratios of calcium to magnesium for the welfare of the plant.

It should also be pointed out here that Hansteen calls attention to the publication after the preparation of his manuscript, of a paper by Krefting in which some light is thrown on the calcium relationships of the brown algae, and namely that the intercellular substance of the brown algae consists of an acid named by Krefting "Tangsäure," and which has the following composition by elements: carbon 39%, hydrogen 5%, oxygen 56%, and which is to be regarded as one of the pectin acids. Krefting shows that with calcium, barium, and strontium "Tangsäure" makes insoluble compounds, while with potassium, sodium or especially with the alkali metals, and also with magnesium in cold and warm water, it forms soluble compounds. It is also believed by Krefting that double salts are produced by this acid with potassium and sodium, for example, or with other metals in a similar way, magnesium also being included in that group. These double salts are all easily soluble, whereas for example, on the other hand, those double salts which it makes with potassium and calcium or with sodium and calcium, or with magnesium and calcium, are very difficultly soluble. The significance of these investigations may be great in the modification of the present established and widely accepted views of Loew with reference to the rôle of calcium and magnesium which we have above discussed. The reader of this paper will perhaps

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also be interested in noting the rather extensive bibliography given by Hansteen in the paper under discussion.

Viewing the question of the lime-magnesia ratio hypothesis in its practical aspects and bearings, one is at once impressed with the hopelessness in general farming particularly, of attempting to maintain a proper lime-magnesia ratio in soils. Assuming that Loew's necessary ratios for different groups of plants are correct, and assuming further that we should have to grow a series of crops, as Meyer points out, like buckwheat, barley, oats and legumes, in rotation, we should have to be constantly changing the ratio of lime to magnesia in a given piece of land from season to season so as to accommodate the lime-magnesia ratio conditions therein to the particular crop which we are growing. How thoroughly infeasible such a scheme would be is evident to anyone without discussion. If we consider, moreover, that we were growing orchard crops, the trees of which had a certain lime-magnesia ratio very far different from the annual crop, and then that we tried to grow intercalary crops between the trees, we should have to change at one and the same time, very probably, in accordance with Loew's idea, two different ratios of lime to magnesia which might vary as much as 4:1 or 5:1, down to 1:1, which is the ratio given for oats by Loew. In practice, therefore, any attention to the lime-magnesia ratio would seem to be quite out of the question even if it were proved that the lime-magnesia ratio for specific plants must necessarily be kept at a certain point.

Wholly irrational as it may seem from the foregoing statements to attempt changing the lime-magnesia ratios in field soils by either applications of calcium or magnesium salts, it has none the less been attempted to a considerable degree in this state, and the writer has known of as much as forty tons of gypsum per acre having been applied to citrus soils for the purpose of bringing up a proper relationship between calcium and magnesium compounds in that soil to meet a supposed optimum ratio for the citrus trees. Needless to say, such applications have never met with favorable results, and considering other disadvantages about gypsum, we can readily see how some of them might meet with very unfavorable results.

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Of course all of these remarks are not to be construed as in any wise derogatory to the practice of liming soils. That, as is plainly evident to all of my colleagues, is quite another story. That liming is necessary on many soils and perhaps one of the important practices in soil management, is beyond cavil. It is only liming or "magnesiaizing" (if I may be allowed to coin a term) for the purpose of establishing certain ratios of lime to magnesia in the soil that I object to.

Unfortunately, the space of this paper will not allow of a fuller critical discussion and analysis of the question of the lime-magnesia ratio and of the investigations and results put forward in support thereof or antagonistic thereto. The following table, however, and the discussion which I have given, appear to me to point pretty clearly to the untenable nature of Loew's hypothesis for either theoretical or practical purposes. The toxic effects of magnesium in excess or when applied to soil, not in excess, are easily explained on the basis of its own specific physiological properties, and need no introduction of "ratio" considerations between itself and calcium to explain them. The non-toxicity of calcium in large quantities, as has been shown time and again in investigations above reviewed and others which can not here be mentioned, renders questionable Loew's attempts to show that calcium in excess, especially in its carbonate form, is toxic, or at least in such a way as magnesium compounds are toxic. That magnesium compounds may be added to excessive quantities of calcium and overcome ill effects of such excessive quantities is rendered at least somewhat questionable by researches which I have reviewed, and where favorable effects are noted, explanations can be made on many other bases which do not require the assumption of something so entirely artificial as the necessity for a proper lime-magnesia ratio. Likewise, in the addition of calcium to excessive quantities of magnesium there is even more opportunity for explaining beneficial effects which usually follow such applications in many other ways, as already indicated above, than by assuming that there is a necessity for a certain lime-magnesia ratio. Calcium and magnesium are of course essential elements in the growth of plants. Their some-

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what similar chemical nature does not give us leave, however, to place them in a similar physiological category, and indeed numerous investigations point to their total dissimilarity so far as that is concerned—Loew's own investigations being perhaps the most important in support of that idea. But despite all of that, it is inconceivable to any one who has in view the modern developments of plant physiology and physical chemistry, as well as the modern views on the soil and its solution, why it should be any more assumed that a proper ratio between calcium and magnesium is necessary than that a proper ratio between calcium and potassium and between calcium and iron and between calcium and other essential elements in the growth of plants, are necessary. A proper understanding of and consideration in connection with this subject of the general principle of antagonism between ions is far more pertinent in this connection, observing how generally the principle applies, in at least partly accounting for beneficial results from the application of lime to magnesia, and for the change thus wrought in their relationship in soils. The balance of the effects which are not accounted for by antagonism between the ions within the soil solution itself, may so far as soils themselves are concerned, be just as easily explained on the basis of the effects of the applications on the physical condition of the soil, on the chemical reactions following in the soil, on the bacterial flora, on the protozoan fauna, and on other faunas within the soil, as it can be by introducing the rather far-fetched notion of the necessity of a certain lime-magnesia ratio.

In brief, the writer believes that he has shown by a review of some of the most important investigations in the field, that in the first place there is little or no evidence in support of the necessity to plants for a proper lime-magnesia ratio in soils, which is specific for certain groups of plants. In the second place, that when certain favorable effects are noted which appear to indicate that they follow from the adjustment of the ratio of lime to magnesia, such favorable effects can easily be explained on many other grounds which do not call at all for the introduction of the hypothesis of the lime-magnesia ratio.

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Positive Investigations

Name of investigator	*Place and date*	*Plants and medium*
Loew	Germany, 1892	
Loew and May	Porto Rico, 1910	Cowpeas, privet, tobacco, barley, oats, wheat, beans. Water, sand and soil cultures
Furuta	Japan, 1902	Cabbage, buckwheat, oats. Soil cultures
K. Aso	Japan, 1902	Barley, soy beans, onions. In pots
K. Aso	Japan, 1903	Mulberry tree. Pot experiments
K. Aso	Japan, 1904	Rice. Pot experiments
Daikuhara	Japan, 1903	Beans. In pots
Nakamura		Barley. In pots
Loew and Aso	Japan, 1905–6	
Daikuhara	Japan, 1905–6	Barley. In pots
Daikuhara	Japan, 1905–6	Rice. In pots
Daikuhara	1905–6	Tobacco plant. In pots
Suzuki	Japan	In pots
Maki and Tanaka	Japan, 1906–7	Barley. In pots
Namikawa	Japan, 1906–7	Flax, spinach
Nakamura	Japan, 1907–8	Mulberry. In pots
Kanomoto	Japan, 1908–9	Oats, rice, barley, buckwheat, mustard, onions
Sirker	Japan, 1909	
Bernardini and Corso	Italy, 1909	Wheat, rye, oats, rice, barley, maize, onions, spinach, flax, cabbage
Bernardini and Siniscalchi	Italy, 1910	Continuation of work—nutritive solutions and pot cultures; lupines, in pots
Warthiadi	Germany, 1912	Solution and sand cultures
Robert Stewart	Utah, 1912	
Voelcker	England, 1912	Wheat. In pots
Loew	1913	Rice

Negative Investigations

Name of investigator	*Place and date*	*Plants and medium*
von Portheim	Vienna, 1901	Cress, sorrel, rye, barley, wheat, oats, larch and pine
Gössel	Marburg, 1903–4	Barley, horse beans. Water cultures. Soil cultures
Dojarenko	Russia	Oats. In field
Meyer	Germany	In pots
Meyer	Germany, 1911	Buckwheat, oats. In pots, clay loam, sand and loam

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Name of investigator	*Place and date*	*Plants and medium*
Konovalov	Russia, 1907–8	Millet and oats, barley, maize. Sand cultures, water cultures
Konovalov	Russia, 1910	Wheat, lupines, *Setaria italica* and oats. Water and sand cultures
Kossovich and Althausen	Russia, 1910	Barley
Wheeler and Hartwell	Rhode Island, 1904	
Lemmermann, Einecke and Fischer	Germany, 1911	
Lemmermann, Foerster and Einecke	Germany, 1911	
Gile	Porto Rico, 1912	Pineapple. In pots
Gile	Porto Rico, 1913	Rice. Culture solutions
Tottingham	Baltimore, 1914	
Gile and C. N. Ageton	Porto Rico, 1913	
Gile and C. N. Ageton	Porto Rico, 1913	Bush beans
Meyer	Germany, 1913	
Maze, Rout and Lemoigne	France, 1913	Corn, lupines, vetch (one species)
Pisciotta	Italy, 1914	
Hutin	Peru, 1914	Cane
Russell	England, 1912	
Hasselhoff	Germany, 1914	In pots
Hopkins	Illinois, 1910	Wheat. Marshal brown silt loam in pots
Meggitt	India	
Miege and Compain		In field
Hilgard and Loughridge	California	Citrus trees. In field

Indifferent Investigations

Name of investigator	*Place and date*	*Plants and medium*
Kearney and Cameron	1902	
Ulbricht		Oats, barley. In field
Ulbricht		Yellow lupine, barley, vetch, radishes
Schreiber	1895–96	Oats and turnips. In field
Loew and Honda	Japan, 1895–96	Conifer trees—*Cryptomeria japonica*, *Thuja obtusa* and *Pinus densiflora*
Heinrich	1896–97	Lupines
Passerini	1897–98	Wheat
D. Meyer		Oats, potatoes, horse beans, vetch, mixture of plants like grass and alfalfa. In pots
Ulbricht		Barley. In pots
R. Averna-Sacca	1913	Grape vines, coffee plants, orange trees. In pots

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MEASUREMENT OF EVAPORATION RATES FOR SHORT TIME INTERVALS

EARL S. JOHNSTON AND BURTON E. LIVINGSTON

The Johns Hopkins University, Baltimore, Md.

One of the peculiarities of the various forms of atmometers[1] so far devised is that they measure rates of a process rather than the conditions prevailing at any given moment. With the barometer and thermometer it is different. Disregarding the lag in the response of the last-named instruments to the conditions measured, each of them furnishes a static measure of surrounding conditions at the time a reading is taken. To obtain a summation or average from such instruments it is necessary to make readings at frequent intervals and then subject the results to mathematical treatment. Recording thermometers and barometers simply record readings at very short time intervals, and the integration and averaging must be accomplished after the record is made. Atmometers, on the other hand, always give the mean rate of the process of evaporation for the time period that has elapsed since the last reading, and it has usually been practically impossible to determine the evaporation rate for very short periods of time. It is clear that this marked difference is due to the fact that thermometers and barometers measure a *condition* (which may be stationary) while atmometers measure a *rate* of change, and such a rate must involve a time period.

Nevertheless, the rate of water-loss from an evaporating surface is determined by a set of conditions that may be regarded as static for any instant, just as static as is temperature or barometric pressure. This set of conditions has been called the

[1] On atmometers, see: Livingston, B. E., Atmometry and the porous cup atmometer. Plant World **18**: 21–30, 51–74, 95–111, 143–149. 1915. Other literature is there cited.

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evaporating power of the air.[2] In both cases the condition considered is of course conceived as dependent upon rates (of molecular motion, etc.), but the present consideration need not enter into these deeper questions.

It must have occurred to most users of atmometers that a form of this instrument that might indicate the magnitude of atmospheric evaporating power from time to time, as readings might be made upon a thermometer, would be exceedingly convenient for many purposes. For example, if it were required to maintain the evaporating power of the air in a room at a constant value, as by manipulating temperature and humidity controls, it would be helpful to be able to read the evaporating power at a glance, just as temperature can be read from an ordinary thermometer. As it is, however, the evaporating power of the air can be determined only in terms of the evaporation rate from a standard surface, requiring two readings with a known time period intervening. With precise methods of measurement the required time period may be comparatively short, but even the porous cup form of atmometer, as usually arranged, is seldom read in practice at intervals of less than ten or fifteen minutes, and the employment of open pans of water generally requires much longer periods. An atmometer that might allow instantaneous determination of the evaporating power of the air would be a valuable instrument for greenhouses and, if it were durable and easily read, it might serve a useful purpose in assembly rooms, living rooms, etc.

It is quite possible to measure a rate without two readings if the rate may be converted into a pressure and thus read upon a manometer scale, and this seems feasible in the case of atmospheric rates. It is only necessary to introduce suitable resistance to water movement in the tube that connects the porous cup with the water reservoir below, and to connect a manometer to

[2] On the use of this term and objections raised thereto, see: Livingston, B. E., Atmospheric influence on evaporation and its direct measurement. Monthly Weather Rev. **43**: 126–131. 1915. *Idem*, A modification of the Bellani porous plate atmometer. Science, n. s. **41**: 872–874. 1915. *Idem*. A single index to represent both moisture and temperature conditions as related to plants. Physiol. Res. **1**: 423–442. 1916.

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a lateral opening in this tube above the resistance. The resistance, at the lower end of the supply tube, should be such that when the manometer registers no suction on the part of the cup the rate of flow of water through the resistance is lower than the lowest rate of evaporation to be dealt with. With higher rates of evaporation suction is developed and the mercury column of the manometer is displaced, while the relatively increased water pressure from without causes a more rapid flow through the resistance in the tube. The greater is the evaporation rate the higher does the mercury rise in the proximal arm of the manometer. Of course the resistance must be small enough so that somewhat less than an atmosphere of pressure may drive water through the tube at a rate as great as will ever need be measured. After proper calibration, a scale may be attached to the manometer of such an arrangement, to be read in terms of cubic centimeters per hour. Any line of this scale represents the rate of water movement through the tube under the pressure indicated by the manometer when its mercury meniscus stands at that line. With changes in the rate of evaporation from the porous cup above, the mercury column rises or falls, and if the manometer is of small diameter (as related to the surface exposed by the cup), the lag in the manometer adjustment is very slight.

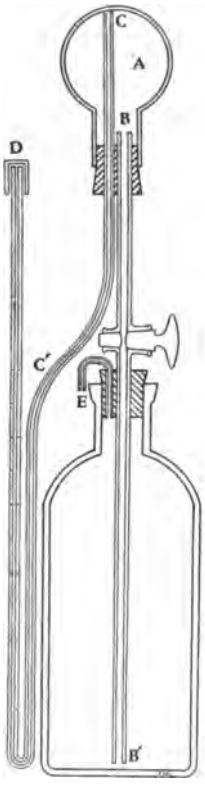

Fig. 1. Porous sphere atmometer with burette attachment. *A*, porous sphere; *B*—*B′*, supply tube (with cock) from reservoir; *C*—*C′*, supply tube from burette; *D*, burette cap; *E*, air-intake. Sphere is filled by suction at open end of burette.

The first instruments of this kind were constructed by one of the writers, assisted by Mr. H. C. Sampson, at the Desert Laboratory in the summer of 1914. The porous cups were arranged on bottles in the ordinary way and two forms of resistance at the lower end of the supply tube were employed. One of these was

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a very fine capillary glass tube, the other was a small porous clay cup attached by a rubber stopper to the free end of the supply tube. Thus all the water passing from the reservoir to the atmometer cup had to pass through the capillary or, in the other case, through the porous walls of the little cup. Cylindrical atmometer cups of the usual form were employed and the manometer was made of glass barometer tubing having a bore of about a millimeter. These instruments operated very satisfactorily at first, but the resistance to water movement always increased with the lapse of time, apparently because of some sort of clogging of the capillary or of the small porous cup, so that readings on the manometer scale soon became unreliable. During the winter of 1915–16, in this Laboratory, the writers experimented further with this kind of apparatus, attempting to devise a form of resistance that would not readily alter, but the attempt was unsuccessful and the whole matter has been laid aside.

If the instrument with a pressure gauge can not as yet be produced, it behooves us to employ the nearest approach thereto that is readily feasible, and such an approach has been carried out by merely employing a device by which the ordinary pair of readings may be made with a very short intervening time period. The essentials of this device are as follows. The atmometer cup is mounted so as to draw water from a finely graduated burette—a straight pipette graduated to hundredths of a cubic centimeter is satisfactory—and this burette is also connected with the regular water-reservoir, but a cock allows water movement through this connection to be cut off entirely. When the cock is open the water level in the burette and that in the reservoir are the same (or but slightly different because of capillarity), and the instrument draws from the combined supply in the usual way, readings for long periods being made by filling through the small burette, from a larger burette or graduated cylinder. When the cock is closed the instrument draws water solely from the small burette, by means of which readings may be made in terms of hundredths of a cubic centimeter. Of course the cock must be reopened before the small burette

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is emptied, when it will refill to the level of the water surface in the reservoir, or slightly above; it is not essential that the burette be filled to the zero mark of its scale. The diagram of figure 1 shows one way of erecting the apparatus.

Such an instrument may be placed in a room or greenhouse, or may be carried from place to place. It may be allowed to operate indefinitely so long as considerable distilled water is always present in the reservoir bottle and so long as the cock is open. Readings may be taken in the ordinary way at hourly, daily or weekly intervals, from which the average evaporating power of the air for the period in question may be readily obtained. When it is desired to make a determination for any short period the cock is closed, the time required for the loss of one or more hundredths of a cubic centimeter is determined by direct observation and the hourly rate is obtained therefrom. Thus, if the time required for a loss of a hundredth of a cubic centimeter were 30 seconds it would mean that the average rate of water loss during that short period had been 1.2 cc. per hour. In general, 36 divided by the number of seconds required for the loss of a hundredth of a cubic centimeter of water gives the hourly rate of water loss. If the temperature of the porous cup changes considerably during the time required for the loss of a unit of water a more or less pronounced error will of course be introduced, on account of thermometer action; since a small change in the temperature of the relatively large water-mass in the cup produces a comparatively large alteration in the level of the water meniscus in the burette. On account of the comparatively short time periods required this temperature change is not generally apt to be considerable, however.

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MY CONCEPTION OF OPUNTIA MACRORHIZA ENGELM.[1]

DAVID GRIFFITHS

Bureau of Plant Industry, Washington, D. C

Opuntia macrorhiza was described by Dr. Engelmann in the Boston Journal of Natural History, volume 6, page 206, 1850. The type plants were collected by Dr. Lindheimer in Texas, in "naked, sterile, rocky places on the upper Guadaloupe" according to the or ginal publication.

The type is in the Engelmann Herbarium of the Missouri Botanical Garden. A very important part of the exhibits in the case is a note from Dr. Lindheimer attached to the type reading, "between the Piccardinalis and Guadaloupe, fruit greenish, very pleasant." Later, in 1856, on page 311 of the third volume of the Proceedings of the American Academy of Arts and Sciences, in discussing the geography of the cactus regions of the United States, Dr. Engelmann refers to the Guadaloupe, the "Pierdenales," and the San Antonio rivers. Upon the modern maps we have the Pedernales, a tributary of the Colorado. It has its origin not far from that of the Guadaloupe and runs approximately parallel to that river for some distance. The main town in this region is the village of Kerrville. The country is a rolling broken region with scrub pines, junipers and oaks abounding. Bare rocky hills and ridges where prickly pear abounds are decidedly characteristic of a large section of this part of Texas. A tuberous-rooted species of *Opuntia* is abundant and conspicuous all through the region and in my opinion it must be *Opuntia macrorhiza*. The type was collected by Lindheimer in 1847. In 1850 and 1851 he sent other material to Dr. Engelmann which he considered the same species and which he secured at New Braunfels. There is very clear evidence, as pointed out by the

[1] Published by authority of the Secretary of Agriculture.

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late Professor Bernard Mackensen,[2] that Lindheimer considered that he was dealing with two species in southern Texas for his material is marked, "Die grosse *Opuntia*," and "Die kleine *Opuntia*," referring, presumably, in the one case to *Opuntia Lindheimerii* and in the other to *Opuntia macrorhiza*. Dr. Engelmann must have been influenced greatly in his determination of species by the opinion of his collector, who was the only one at that time who had a field knowledge of the species. My investigations show clearly that the upper Guadaloupe and New

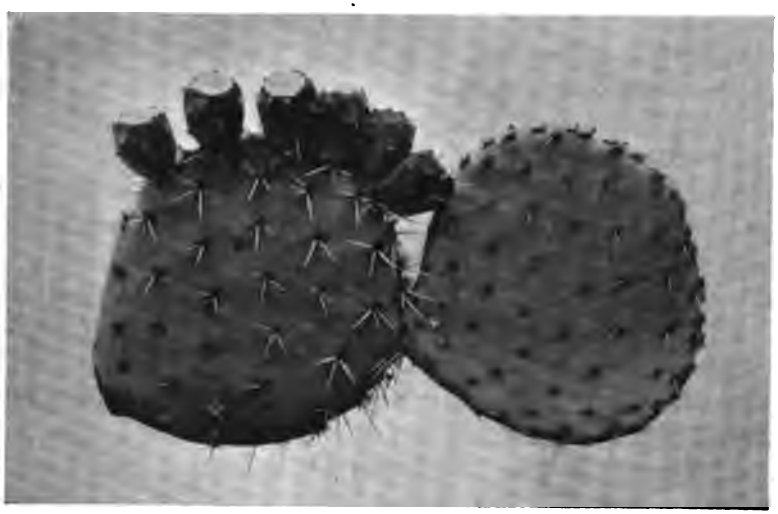

Fig. 1. Two joints with ripe fruits of *Opuntia macrorhiza* grown at Chico, California. One-eighth natural size.

Braunfels tuberous-rooted *Opuntias* are entirely different species, although I believe it is quite possible that the true *Opuntia macrorhiza* may be found on the Edwards Plateau not far from New Braunfels.

In the Cactaceae of the Mexican Boundary Survey Dr. Engelmann seems to have ignored the upper Guadaloupe material entirely, for in his notes he speaks of the species "between San Antonio and Austin (Lindheimer)" and in his figures this is

[2] Bull. Torr. Bot. Club. **39**: 289–290. 1912.

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clearly the one that is illustrated. He is here no doubt following the opinions of Dr. Lindheimer. But it is the upper Guadaloupe plant that is the type of the species and the subsequent errors in interpretation do not affect the case in the least.

Professor Mackensen collected and studied some of the species of *Opuntia* on the rocky knolls east of Kerrville in 1909. From his material Dr. J. N. Rose named and figured a tuberous-rooted species in his honor. Professor Mackensen, shortly before his death, informed me that *Opuntia Mackensenii* is the common, large, tuberous-rooted species of the Kerrville region, and that he secured the type a short distance to the eastward from the

Fig. 2. Two plants of *Opuntia macrorhiza* under cultivation at Chico, California.

corporate limits of the town. When I asked for a definite locality the Professor simply remarked that one could not miss it, that it was the conspicuous thing all around Kerrville.

During the past ten years I have become rather familiar with this region and its species of *Opuntia* and at present have the most of the forms in cultivation, including material from Professor Mackensen's type collection at Kerrville. The region fr m San Antonio to San Angelo and eastward to Temple and Waco has been frequently visited. *Opuntia macrorhiza* has been collected at Kerrville, Brownwood, San Saba, Lampasas, Marble Falls, and Leon Springs. The species while variable is not easily confused with anything else, and is the most common tuberous-rooted species of the region.

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The descriptions of *Opuntia macrorhiza*[3] and *Opuntia Mackensenii*[4] agree very well. In the latter, which seems to be a slight abridgement of a manuscript in Professor Mackensen's hand, it is stated that the flowers are yellow, in the former yellow with reddish base. This latter condition is described in Professor Mackensen's manuscript as "light reddish-brown centered." There is some confusion in words as to the fruit but that might easily have occurred. In the original description of *Opuntia macrorhiza* no mention is made of the exterior color of the fruit, but later[5] Dr. Engelmann, evidently from the same material, adds that the fruit is green or pale-purple, which has no contradiction of "rose-purple with a nearly colorless, pleasant-tasted pulp" which is predicated of *Opuntia Mackensenii.* This statement is exactly that of Mackensen's manuscript description. A copy of my own notes on this point, taken from cultivated specimens from Kerrville, are as follows: 'Fruit a rather light purplish-red with bloom remaining through early maturity, rind greenish and pulp colored a little—rather mottled."

To summarize, there is clear evidence, both descriptive and geographical, that the common tuberous-rooted *Opuntia* of the rocky knolls between the Guadaloupe and the Pedernalis (Piccardinales, Pierdenalis) is *Opuntia macrorhiza;* that the figures in Plate 69 of the Cactaceae of the Mexican Boundary Survey pertain to an entirely different species; and that *Opuntia Mackensenii* is synonymous with *Opuntia macrorhiza.*

The true *Opuntia macrorhiza* has not been treated by me heretofore in any of my publications. In one case[6] the name was erroneously applied to what has since been, in part at least, named *Opuntia leptocarpa.*[7]

There still remains the task of accounting for the plant figured in Plate 69 of the Cactaceae of the Mexican Boundary Survey. But this is another and very different story which will be treated later.

[3] Boston Jour. Nat. Hist. **6**: 206. 1850.
[4] Contr. Nat. Herb. **13**: 310. 1911.
[5] Proc. Amer. Acad. Arts and Sci. **3**: 296. 1856.
[6] New Mex. Coll. Agr. Bull. **60**: 58–59. 1906.
[7] Bull. Torr. Bot. Club. **38**: 141–142. 1911.

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BOOKS AND CURRENT LITERATURE

BALANCE IN NUTRIENT MEDIA.—Tottingham[1] has studied the influence exerted upon the growth of young wheat plants by a wide range of proportions of component salts in nutrient solutions, and also the modifications in this influence which are produced by different total concentrations. The effect of chemicals upon plant growth may be altered by changing either (1) the concentration of the solution, or (2) the nature or proportions of the component substances. Both of these considerations are dealt with in this paper. The seedlings were grown in water culture, in 250 cc. wide-mouth bottles, for a period of 24 days. They were supported, 6 in a culture, in a newly devised 2-piece cork stopper. The solutions were renewed every 3 days. The paper includes a very thorough review of the literature and a rather complete bibliography.

The nutrient salts used were those composing Knop's well-known nutrient solution—KH_2PO_4 or K_2HPO_4, $MgSO_4$, $Ca(NO_3)_2$, and KNO_3. A preliminary study showed that Knop's solution employing K_2HPO_4 and having a total concentration of 2.2% will stand without precipitating for a period of 3 or 4 days, at temperatures between 20° and 23°C.; while when KH_2PO_4 was employed the maximal concentration to stand for this length of time was 2.8%. The precipitate forming in more concentrated solutions was found to be mainly $CaSO_4 . 2 H_2O$.

Tottingham's first series dealt with the effect of different total osmotic concentrations of Knop's solution, these concentrations being calculated approximately by means of published data on electrolytic dissociation and osmotic pressure. Nearly equal dry yields of tops were obtained in solutions ranging in osmotic concentration from 0.25 to 3.25 atmospheres. Solutions in which KH_2PO_4 was used gave about 18% greater top yields than those in which K_2HPO_4 was employed. On this basis, therefore, KH_2PO_4 was used in the following experiments.

In the principal part of the study various proportions of the four salts were employed in solutions with three different osmotic concentrations. These concentrations were chosen so as to have the medium

[1] Tottingham, W. E., A quantitative chemical and physiological study of nutrient solutions for plant cultures. Physiol. Res. 1: 133–245. 1914.

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one (2.50 atm.) near the optimal concentration for plant growth, while the lowest (0.05 atm.) was well below and the highest (8.15 atm.) was well above the optimal concentration. For each of these three series the total osmotic concentration was considered as divided into ten equal parts, and these tenths were distributed among the four component salts in all possible ways; each series thus contained 84 cultures, all of which had the same total osmotic concentration. Thus in the various solutions of a series, from 1 to 7 tenths of the total osmotic concentration was due to each of the four constituent salts, but no two solutions contained the same proportions of the four salts. To represent the different salt proportions in the various solutions of a series a tetrahedral diagram, composed of seven plane triangular diagrams, was used. These diagrams also served as charts upon which the plant measurements, such as dry weight, etc., were plotted.

A trace of iron, as ferric phosphate, was added to each culture, and a control culture in distilled water was included in each series. The evaporating power of the air was measured during each of these experiments by means of a cylindrical porous cup atmometer, and the relative water loss by transpiration was measured for selected cultures for a period at the close of each experiment.

In the series of optimal concentration (2.50 atm.) the solution producing the greatest dry weight of tops was 11% superior, by this criterion, to Knop's solution of the same osmotic concentration. The volume-molecular partial concentrations of the four salts in this best solution were: KNO_3, 0.00488 m; KH_2PO_4, 0.01551 m; $Ca(NO_3)_2$, 0.01440 m; and MgSO, 0.01660 m. The solution giving the greatest dry weight of roots was 29% superior to Knop's solution, but this was not the same solution as that giving the greatest dry weight of tops. In the suboptimal series (0.05 atm.) a still more marked improvement over Knop's salt-proportions was obtained. The best solution for the growth of tops gave a top yield 39% greater than Knop's, while another solution of this series gave 15% better root growth.

Similarly, salt proportions superior to those used by Knop were found in the series of supra-optimal concentration, which had a calculated osmotic concentration of 8.15 atmospheres. Shive's[2] cryoscopic determinations showed that Tottingham's calculation gives too high concentrations for these solutions, the average value obtained by Shive being 7.22 atmospheres. For the optimal and suboptimal series Shive's

[2] Shive, J. W., The freezing points of Tottingham's nutrient solutions. Plant World 17: 345–353. 1914.

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results agreed with the calculated osmotic values, as nearly as could be measured by the cryoscopic method. The increase in yield in the best solution of Tottingham's supra-optimal series was 53% and 47%, for tops and roots, respectively, over the yield from Knop's solution of this concentration.

In the solutions giving the highest dry weight of tops the Mg/Ca ratio was 1 : 1 for the optimal, 2 : 1 for the suboptimal, and 3.3 : 1 for the supra-optimal concentration, while in Knop's solution this ratio is 1 : 3. An apparently characteristic form of leaf injury was observed with the highest values of this ratio in the optimal and supra-optimal series. A decrease in transpiring power attended severe injury of this kind. Also, in the supra-optimal series another form of leaf injury accompanied the lowest values of the Mg/Ca ratio.

Tottingham's discussion brings out the fact that the effect of a mixture of salts in solution upon the amount of dry matter produced and upon the development of the plant in general, depends upon the complex balance of all of the salts in the solution, and not simply upon the ratio of one substance to another; and also that the effect of a given set of the proportions of the nutrient salts varies with the total concentration of the nutrient solution.

If any feature of the experimentation here reviewed is to be adversely criticized it is perhaps the employment of distilled water as a control medium; since plants growing in distilled water soon become unhealthy, this cannot be considered a perfect control. A more satisfactory control medium should give healthy plants that continue to grow and respond to external conditions throughout the period of a given experiment. This and other points in the technique employed will of course become more refined as more work of this kind is done. On the whole this investigation appears to be the most thorough study of its kind that has yet appeared, and perhaps its most valuable feature is the method developed for studying the comparative effects of complex salt solutions in a logically complete way.—SAM F. TRELEASE.

TEMPERATURE AND THE RATE OF GROWTH.—Leitch has recently completed a study of growth in pea roots, as affected by temperature, in the laboratory for plant physiology of the University of Copenhagen. It was found that the relation of growth to temperature between 2°C.[1] and 29°C. is to be expressed by a curve similar to that of respiration

[1] Leitch, I., Some experiments on the influence of temperature on the rate of growth in *Pisum sativum*. Ann. Bot. **30**: 25–46, January, 1916.

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or general metabolism, rather than by the van't Hof formula. Above the higher temperature named the plotted rate is a series of broken lines. Leitch was unable to find any effect from simple changes in temperature; his growing material appeared to assume the rate pertaining to any new intensity, without shock or stimulatory effects. It is to be supposed that the diverse conclusions on this matter are probably referable to unlike conditions of humidity or food supply, rather than to auxetic processes. Four cardinal points are distinguished, the *Minimum*, at which growth may take place, 2°C. in *Pisum;* the *Maximum*, the highest, 44.5°C. in *Pisum*, the *Optimum*, the point at which the highest constant rate occurs, betwen 28 and 30°C. and the *Maximum rate* point, at which the process may attain its highest intensity, but is not maintained. In *Pisum* this occurs at about 30.3°C. and begins to decrease after ten minutes of exposure. It is obvious that this conception may express some of the facts upon which conclusions as to stimulatory effects might be based. It is notable that Leitch was unable to detect any effect of light on the growth of the roots although but little attention was given to this phase of the subject.—D. T. M.

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NOTES AND COMMENT

On April 20 the cornerstone of the laboratory building of the Brooklyn Botanic Garden was laid with brief formalities. Addresses were made by the President of the Brooklyn Institute of Arts and Sciences, of which the Garden is a department; by Dr. C. Stuart Gager, Director of the Garden; and by Mr. Alfred T. White, through whose instrumentality a private gift of $100,000 was obtained, thus securing a municipal appropriation of like amount and making possible the completion of the laboratory building and a range of plant houses. The total estimated cost of these structures is $270,000, and it is anticipated that they will be completed by the end of this year. The laboratory building will contain the offices of administration; the library, comprising about 3800 books and 5900 pamphlets; the herbarium, comprising at present over 110,000 sheets; a lecture hall seating 574 persons; two class rooms; morphological, physiological, and elementary laboratories; a photographic room; and ten private research rooms. The basement will contain a physiological dark room, a constant temperature room, and a culture room with "hospital finish," permitting ready sterilization.

The addition of a new tract of about six acres of land has made possible the enlargement of the general systematic plantations of the Garden. One or more beds are devoted to each plant family, with enclosures formed by shrubs which are related to the herbaceous plants in the beds. Other sections include a native wild flower garden, an economic garden, and sections for experimental evolution and plant breeding.

The trustees have recently established the first of a number of research fellowships and have authorized the appointment of the first of a number of resident investigators. Prof. W. H. Rankin, of Cornell University, has been appointed Research Fellow for 1916 and 1917, and will undertake a survey of the diseases of trees and shrubs in the parks of Brooklyn. Dr R. C. Benedict has been appointed Resident Investigator and is making a study of the Boston fern, *Nephrolepis*, and the behavior of its varieties. An arrangement has been made with New York University by which the research courses in botany at that institution will be conducted at the Brooklyn Botanic Garden. The facilities at the Garden for plant breeding and plant pathology will determine the principal fields of work under this arrangement.

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Prof. Edward J. Russel, Director of the Rothamsted Experimental Station, Harpenden, England, has prepared a new edition of Soil Conditions and Plant Growth. The first edition of this work (see review in THE PLANT WORLD, Vol. 16, p. 97) has taken an important place in the literature of pedology, and the publishers (Longmans, Green and Company) are performing a service in keeping it abreast of current work. Numerous minor changes and additions have been made, and a chapter has been added on The Relationship between the Microorganic Population of the Soil and the Growth of Plants.

The eighth edition of Goff's *Principles of Plant Culture* has just been issued, revised by Prof. J. G. Moore and Prof. L. R. Jones (The Macmillan Company). This useful book adheres rather closely to its former scope and treatment, being an elementary presentation of practical plant physiology and of the management and propagation of economic plants. The physiology in this edition appears to be sound and up to date, in spite of the tendency to state that "nature provides" for this and that.

A semi-popular manual of the trees of Texas has been prepared by Dr. Isaac M. Lewis, of the Univesity of Texas (Bull. Univ. Tex. 22, 1915). Over 200 native species are described, and many of these are illustrated. The bulletin is in no sense a critical taxonomic review of the Texan silva, and it contains very little fresh information as to the distribution and ecological behavior of the trees, but it will nevertheless be a very useful publication both in and out of Texas.

Mr. E. A. Goldman, Dr. H. H. T. Jackson, and Mr. Walter P. Taylor, of the Biological Survey, have left Washington for the San Carlos Indian Reservation, Arizona, and will be engaged during the summer in a continuation of the field work in animal and plant distribution which has been in progress in that state for several seasons.

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A STUDY OF THE RELATION OF SOIL MOISTURE TO TRANSPIRATION AND PHOTOSYNTHESIS IN THE CORN PLANT

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The object of the following experiments was to determine the relation existing between the amount of transpiration and of photosynthesis in corn plants and the degree of soil moisture in which they were grown. Three degrees of soil moisture were maintained. The amount of transpiration was obtained by continuous weighings of potometers and a record was kept of the water that was used by the plants. The amount of photosynthesis was determined by measuring the weights of a given unit of area of the plants of the three series of soil moisture at different intervals during the day. The plants were grown in the greenhouses of the University of Nebraska during the fall and winter of 1914–1915 under normal greenhouse conditions. In the progress of this work the writer has become deeply indebted to Dr. R. J. Pool.

EXPERIMENTAL METHODS

Kind of potometers used and their preparation. Two-gallon glazed earthenware crocks such as can be purchased at a crockery store were employed throughout the experiments. These, being glazed, were evaporation proof. A good grade of loam soil was well worked over with a rake and then sifted through a mesh of $\frac{3}{8}$ in. which gave a very fine grade of loam soil free from lumps and foreign matter. To facilitate the spread of water throughout the entire potometer a layer 3 cm. deep of medium size gravel was placed in the bottom of each potometer. One 3 in. unglazed earthenware flower pot (common greenhouse potting pot) was filled with gravel and inverted in each of the potometers. A

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5 mm. glass tube was inserted to a depth of about 5 cm. through the hole in the bottom of the flower pot. The glass tube was left long enough to extend above the level of the top of the potometer. This tube was used for watering. Another glass tube 10 mm. in diameter was placed with one end in the gravel layer and the other extending a few centimeters out of the potometer. This latter tube was for the purpose of aeration. The loam soil was then added to within 5 cm. of the potometer top and jarred down slightly to render the soil mass homogenous (see fig. 1).

Starting the potometers and establishing initial moisture content. The corn plants were started in flats of loam soil. When they

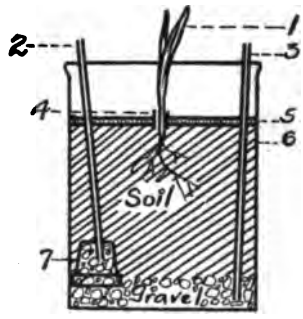

Fig. 1. Diagram of potometer. *1*, plant; *2*, watering tube; *3*, aerating tube; *4*, paper collar; *5*, wax seal; *6*, glazed crock; *7*, flower pot.

were approximately 2 inches high they were transplanted, five to a potometer, the weaklings being discarded. Four plants were run in each potometer, but five gave an opportunity of discarding a weak one before sealing. After transplanting, the plants were watered by pouring equal amounts of water into each potometer by means of the tube for that purpose. As soon as the seedlings were making a good growth they were allowed to go without watering until the plants showed signs of wilting. This was taken as the lowest moisture content at which they would grow. 25 cc. of water was then added to each potometer in order that the plants would be slightly above the wilting point. Trials were then made with similar amounts of soil and it was found that 500 cc. of water would render the amount of soil con-

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tained in the potometers as moist as the plants would probably stand. This amount was added to potometers for the high moisture content. 250 cc. of water was then added to other potometers for the intermediate degree of saturation. Soil samples of the three series showed a low content of 25%, a medium of 45% and a high of 65% of the possible saturation.

Sealing the potometers. The wax-seal method was used. To prepare this seal 80 parts of paraffin (50°) were melted together

Fig. 2. View in greenhouse showing the cultures, scales, and method of weighing.

with 20 parts of petrolatum to just above the melting point o the mixture. Small paper collars were made by rolling her barium paper over a glass tube and glueing it in the form of the tube. When the glue had set the paper tube was removed and cut up into 2 cm. lengths. One of these collars was put around each plant and pressed slightly into the soil to give it stability. Sufficient of the wax was poured on each potometer to give a seal of 5 mm. thickness. The crock was rocked slightly to insure a

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complete seal at the edges. The space in the paper collar around each plant was filled with a fine grade of sand for the purpose of reducing evaporation. In a seal of this kind no paraffin comes in contact with the plant and it was found by checks that it was impossible to detect any loss of water from such a seal.

Watering and weighing. The plants were watered by means of a graduate and a funnel. The correct amount of water to be added, determined by weighing, was measured into the graduate and added to the potometers through the tube for that purpose. The weighing was done with what is known as a "micrometer" scale. This scale weighs accurately to within five grams up to eighteen kilos, and proved very efficient for rapid weighing.

TRANSPIRATION EXPERIMENTS

These were made to determine the correlation existing between the amount of water transpired per unit area of leaf surface and the moisture content of the soil. Also to determine the water equivalent of the plants, or the ratio of dry matter produced to the amount of water used by the plants under the various moisture contents of the soil.

The potometers in the series run for the day and night transpiration were watered at each night weighing. The others were weighed and watered every other day during the greater portion of the period of the experiment. The last two weeks, however, when the plants were transpiring greater amounts, due to increased area of transpiratory surface, they were watered each day. To compensate for the increase in weight of the plants by growth it was figured by previous experiments that approximately one gram of material per plant was added each day. Therefore, at intervals of ten days sufficient water was added to make up for the increased weight of the crop. This was merely for the purpose of reducing error. One series of thirty potometers was weighed both morning and night to determine the relation of nocturnal to diurnal transpiration. The weighings were taken as nearly as possible at the same time of day each time for the morning and night weighings so that the amount of error would be as small as possible. The potometers of the three

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series were intermingled in such a manner that the plants of any one series would not be subjected to conditions varying from those of the others. When an experiment was completed the plants were severed at the crown, and tracings made of them upon paper. They were then steamed to stop the respiratory processes and placed in a drier where they remained until they had attained a constant weight. The area of the leaves was

Fig. 3. One potometer from each soil saturation series. Plants between six and seven weeks old. The dry culture is on the left, the medium in the middle and the wet on the right.

then determined by means of the leaf tracings and a planimeter. The dry weight of the plants without the roots was obtained, and this datum was used in the calculation of the water requirement of the crop.

The relation between the day and night transpiration is shown in Table 2 and figure 4. It will be noted that the amount transpired during both day and night periods show the same relation to the degree of soil moisture, *i.e.*, the plants grown in the

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65% saturation transpired the greatest amount for both day and night, the plants in the 25% saturation the least, while the ones in the 45% saturation were intermediate. This relation remained quite constant throughout the experiment with the least amount of variation occurring in the night periods. A great variation occurred in the amount transpired from day to day, but this was quite constant for the three series and was probably due to variations of those factors which favor transpiration as

TABLE 1

Rates of transpiration at different degrees of soil moisture

EXP. NO.	NO. POTS	PER CENT SOIL SATURATION	DRY WEIGHT	LENGTH OF EXPERIMENT	GM^2H	H_2O REQ.	AREA LEAVES
			gms.	*hrs.*			*sq. cm.*
1	10	25	36.147	843	5.5	205	16,030
	10	45	32.100	843	6.4	272	16,010
	10	65	31.466	843	8.8	330	13,900
2	20	25	195.96	1320	4.4	180	59,406
	20	45	225.51	1320	5.2	226	73,452
	20	65	237.69	1320	5.7	261	82,380

TABLE 2

Rates of diurnal and nocturnal transpiration at different degrees of soil moisture

NO. POTS	PER CENT SOIL SATURATION	LENGTH OF EXPERIMENT	LEAF AREA	AMOUNT TRANSPIRATION		RATE GM^2H	
				Day	Night	Day	Night
		hrs.	*sq. cm.*	*gms.*	*gms.*		
10	25	552	31,670	11,105	1,860	6.3	1.1
10	45	552	34,105	12,830	2,605	7.3	1.4
10	65	552	38,409	17,075	3,730	8.0	1.7

heat, moisture deficit in the atmosphere, etc. The amount transpired increased measurably from day to day for the day periods due to increased growth and consequently transpiratory surface. The increase for the day periods was more than 100%, but in the case of the night transpiration the increase was much less, being not more than 20% for the period. Apparently, therefore, the plants were transpiring less per unit area during the night periods the larger they became.

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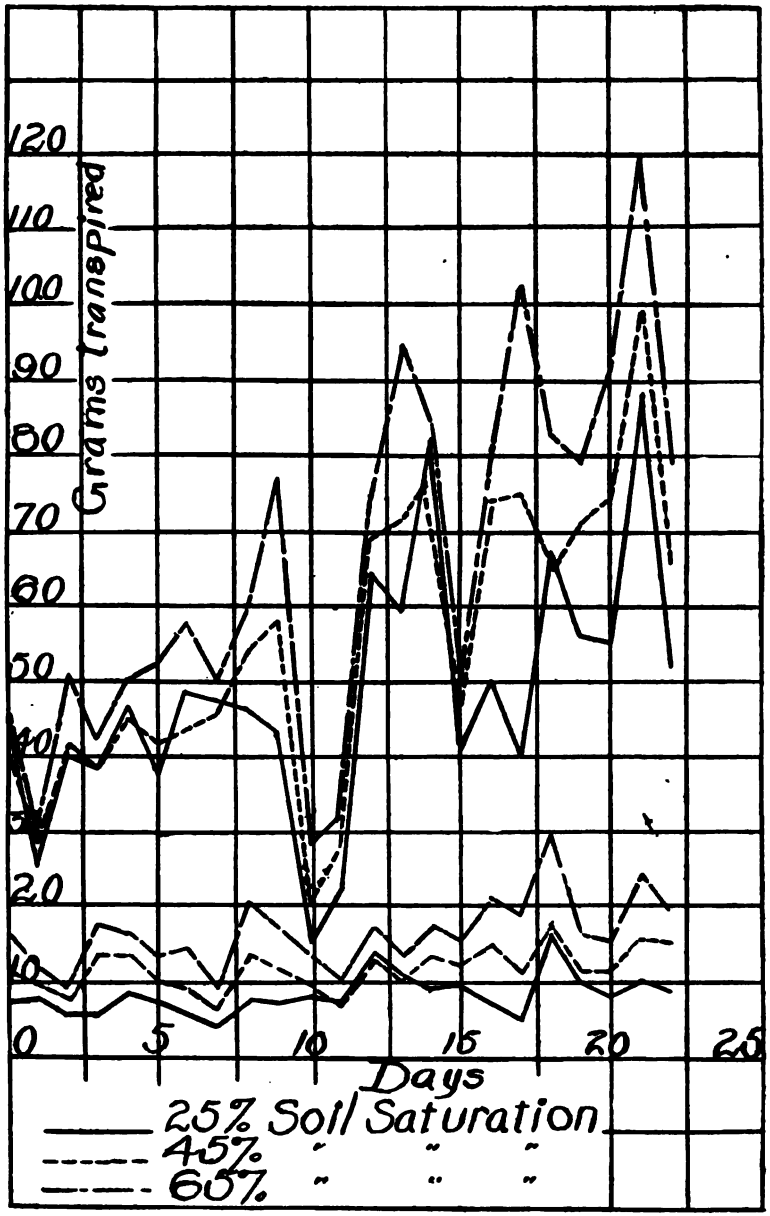

Fig. 4. Curves showing comparison in the amounts of transpiration between the three degrees of soil moisture. The upper set of curves show the rates for the daylight hours, the lower for the night.

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It will be noted in Table I that in the first experiment the water requirement is somewhat higher than for the later experiment. This can be accounted for by the fact that the plants in the first experiment were younger and growing much faster than those in the later. The figures in both cases show a constant relationship between the series. The rate of transpiration in GM^2H[1] shows the same relation to moisture content as does the water requirement, as one would naturally expect, for the more water lost in GM^2H would indicate the greater amount the plant would use in the production of a given amount of organic material. The rate of transpiration in GM^2H for the day and night series shows a greater amount per unit area, but this is undoubtedly due to the fact that this series was run at a time when there was a greater amount of sunshine and conditions for transpiration were better than for the other series.

PHOTOSYNTHESIS EXPERIMENTS

The object of these experiments was to determine the relation between the weights per unit area of leaf surface at different periods of the day and the three percentages of soil saturation. To obtain these data it was essential to obtain leaf clippings at regular intervals. Six-hour intervals was considered as being sufficiently frequent. The plants were placed in a convenient position on the greenhouse bench and, starting at 6.00 p.m. clippings were made every six hours until the following day at 6.00 p.m., making five clippings in all that were taken for each experiment. In taking the clippings two leaves were removed from each potometer of four plants. At each succeeding period the clippings were taken as nearly similar to the preceding ones as it was possible to do. After each set of clippings was made they were taken immediately to the laboratory where tracings were made of them from which the size was obtained. The leaves were steamed thoroughly, dried and from the area of the leaves, the amount of leaf substance, by weight, per given unit of area was obtained.

[1] The expression GM^2H indicates the reduction of the transpiration data to grams of loss per square meter per hour.

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TABLE 3

Data on photosynthesis at different degrees of soil moisture. Experiment I

NO. POTS	TIME CUTTINGS TAKEN	DRY WEIGHT OF CUTTINGS	SIZE OF CUTTINGS	WEIGHT 1 SQ. CM.	PER CENT SOIL SATURATION	AVERAGE WEIGHT 1 SQ. CM.
		gms.	*sq. cm.*	*gms.*		
5	5.00 p.m.	1.333	831.40	0.00160	25	0.00157
	11.00 p.m.	1.258	808.83	0.00155		
	5.00 a.m.	1.416	985.56	0.00143		
	11.00 a.m.	1.495	953.31	0.00156		
	5.00 p.m.	1.690	991.91	0.00170		
5	5.00 p.m.	0.930	622.42	0.00149	45	0.00146
	11.00 p.m.	1.277	952.66	0.00134		
	5.00 a.m.	1.280	976.53	0.00132		
	11.00 a.m.	1.493	969.43	0.00154		
	5.00 p.m.	1.552	968.79	0.00160		
5	5.00 p.m.	1.090	560.50	0.00196	65	0.00156
	11.00 p.m.	1.195	849.46	0.00140		
	5.00 a.m.	1.175	878.45	0.00133		
	11.00 a.m.	1.424.	922.35	0.00154		
	5.00 p.m.	1.570	988.78	0.00158		

TABLE 4

Data on photosynthesis at different degrees of soil moisture. Experiment II

NO. POTS	TIME CUTTINGS TAKEN	DRY WEIGHT OF CUTTINGS	SIZE OF CUTTINGS	WEIGHT 1 SQ. CM.	PER CENT SOIL SATURATION	AVERAGE WEIGHT 1 SQ. CM.
		gms.	*sq. cm.*	*gms.*		
5	6.00 p.m.	3.582	1616.37	0.00221	25	0.00228
	12.00 m.	3.423	1626.05	0.00210		
	6.00 a.m.	3.133	1498.24	0.00209		
	12.00 m.	3.098	1208.09	0.00256		
	6.00 p.m.	4.110	1675.71	0.00245		
5	6.00 p.m.	3.514	1790.52	0.00196	45	0.00209
	12.00 m.	3.105	1648.62	0.00188		
	6.00 a.m.	2.860	1451.90	0.00197		
	12.00 m.	4.003	1688.61	0.00236		
	6.00 p.m.	4.077	1773.11	0.00229		
5	6.00 p.m.	3.415	1722.15	0.00198	65	0.00197
	12.00 m.	2.898	1568.00	0.00184		
	6.00 a.m.	2.645	1532.52	0.00172		
	12.00 m	3.018	1429.32	0.00211		
	6.00 p.m.	4.096	1862.12	0.00219		

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It will be noted in Tables 3 and 4 that the dry series for the most part weighed the most per unit area while the wet series weighed the least, the medium series were intermediate. This was due in part, probably, to the fact that the plants in the moistest conditions were making a more rapid growth. Their tissues would, therefore, be more succulent and less compact than those of the drier series. The plants in the moister conditions due to the accelerated growth were respiring more rapidly and using the organic substances much faster than those of the drier conditions.

In comparing the results obtained in the transpiration experiments with those of the photosynthetic it will be seen that the greater amount of dry matter per unit area is produced in those plants that show the lesser amount of transpiration. Thus it appears that the amount of organic substance formed is not at all proportional to transpiration, as has been held by some authors.

After each series were completed the soil was removed from the potometers and all the soil taken from any one saturation series was thoroughly mixed and a sample taken to determine the final soil saturation. It was found that the moisture content did not vary more than from 1–5% from the initial percentage of saturation.

SUMMARY AND CONCLUSIONS

1. Hogue's Yellow Dent variety of corn was used in these experiments.

2. Three degrees of soil moisture were maintained, viz.: 25%, 45%, and 65% of possible saturation.

3. Glazed earthenware pots were used and filled to a depth of 5 cm. with gravel and an inverted flower pot to facilitate the spread of water.

4. A paraffin wax seal which does not come in contact with the plants was used in the experiments.

5. Leaf areas were figured by the use of a planimeter from tracings made of the leaves before drying.

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6. The water requirement was less for plants in the drier cultures in all experiments, being least in the 25%, most in the 65% and with the 45% intermediate. The rate of transpiration in GM^2H showed the same relation to moisture content as did the water requirement. Thus it appears that the amount of organic substances formed is not at all proportional to transpiration.

7. The nocturnal transpiration showed the same relationship for the three series as the diurnal and the day to the night gave an approximate ratio of 6 : 1 for all three series.

8. A great variation occurred in the amount of water transpired from day to day due to changing environmental conditions, but this change seemed to be approximately constant for the three series.

9. The relative photosynthetic activity was determined by weighing unit leaf areas from the different cultures from time to time.

10. Plants in the dry soil weighed most per unit area, the medium next and the wet the least. The maximum increase in dry weight per unit area occurred about noon with a slight decrease from this to evening. After dark there is a gradual decrease in dry weight per unit area until daylight, the greatest loss occurring before midnight. The relation between the three cultures remained approximately the same for the twenty-four hours.

11. Final soil samples taken at the conclusion of the experiments showed a slight variation of from 1% to 5% from the initial moisture content.

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THE FORESTS OF THE HAWAIIAN ISLANDS

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The Hawaiian Archipelago, formerly known as the Sandwich Islands, remote and isolated in the vast stretches of the North Pacific, has long enjoyed botanical fame for the endemic character of its flora. Its arborescent lobelias, violets, and composites are widely known among phytogeographers. There is no other region of equal area in the world that possesses so large a proportion of peculiar and endemic plant species. Inasmuch as the native vegetation is in the main perennial, woody, and arborescent, this endemic quality is particularly noticeable in the Hawaiian forests. A lumberman from Georgia, from Michigan, or from Oregon, would find in Hawaiian woodlands not a single familiar tree, not a single conifer, and but few species that even faintly resemble those of continental forests.

In any discussion of the Hawaiian forests it is necessary to recognize the various types or classes of forest. These are dependent upon two fundamental factors that profoundly affect the geographic distribution of all the insular plant and animal life. The first factor is topographic—elevation—and is due to the mountainous character of the islands. The islands themselves are but the summits of a titanic submerged volcanic mountain chain. Their peaks rise above the sea from 3000 to 14,000 feet. The second factor is meteorologic—the trade winds, which blow from the northeast practically continuously throughout the year. These winds give each of the islands distinctive windward and leeward climates. The trade winds are heavily water-charged and upon coming into contact with the upper mountain slopes excessive precipitation results, in some places amounting to 400 or 500 inches per annum. The leeward regions, shut off by the mountains from these rain-bearing winds, are arid, in some places having the aspect of veritable deserts.

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Utilizing these two basic factors of elevation and precipitation for a normal classification of the forests, the following well-defined types may be distinguished:

1. *Littoral.*

a. Humid littoral (windward).

b. Arid littoral (leeward).

Fig. 1. View from a mountain slope, showing characteristic arborescent vegetation of lower forest zone (left). A trail through the native Hawaiian forest (right).

2. *Lowlands* (up to 1000 to 1500 feet; elevation varying on the different islands).

a. Humid lowlands (windward).

b. Arid lowlands (leeward).

3. *Lower Forest Zone* (1000 to 2000 feet; variable).

a. Humid section.

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b. Arid sections.

4. *Middle Forest Zone* (1800 to 5000 feet; variable).

a. Humid sections.

b. Arid sections.

5. *Upper Forest Zone* (5000 to 10,000 feet; variable).

6. *Bog Zone* (peaks rising into the cloud belt).

Each zone and section in inhabited by representative trees and shrubs, that attain their best development in their respective areas, and in many instances occur in no other regions. Many Hawaiian trees and other plants are highly precinctive. The kamani (*Calophyllum inophyllum* Linn) is distinctive of the humid littoral; the beach sandalwood (*Santalum Freycinetianum* Gaud. *var. littorale* Hillb.) of the arid littoral; the hau (*Hibiscus tilaceus* Linn) of the humid lowlands; the wili-wili (*Erythrina monosperma* Gaud.) of the arid lowlands; the kukui (*Aleurites moluccana* (L) Willd.) of the lower forest; lehua ohia (*Metrosideros polymorpha* Gaud.) and koa (*Acacia koa* Gray) of the middle forest; and mamani (*Sophora chrysophylla* Seem) of the upper forest.

From the standpoint of lumber supply, the only forests of value are those of the *ohia* and *koa*. Great tracts of *ohia* occur in the Puna district, on the island of Hawaii. These forests have been cut for a number of years by local lumber companies. The *ohia* here attains a height of seventy-five to one hundred feet; the wood is dark red, close grained, hard, and very durable. It has come into local prominence for flooring, railroad ties, paving blocks, and other uses that require hardness and durability. For many purposes it is superior to the best oak. In the vicinity of the famous active volcano Kilauea, on Hawaii, are extensive groves of large *koa* or "Hawaiian mahogany." These have been cut over, as the beautiful golden red wood is prized for fine cabinet work, furniture and interior finishing. The *kukui* or candle-nut is a conspicuous and abundant tree in the lower forests of the various islands, but its wood is weak, coarse-grained, and of little lumber value. Numerous commercial efforts have been promoted to establish the *kukui* oil industry in Hawaii, hut as yet these have not met with success.

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The nuts yield an excellent quality of "wood-oil," but the expense of gathering the crop has retarded commercial exploitation.

On the lowlands the introduced mesquite or *kiawe*, (*Prosopis juliflora*), has been widely spread through the agency of cattle. The tree forms extensive groves and thickets, and the sweet pods are relished by live stock. The pods or "beans" are handled commercially as stock feed, and several local companies grind them, as this process breaks the hard seed coats, and greatly increases the nutritive value. The *kiawe* is also important as a

Fig. 2. Ancient kukui or candlenut trees.

local source of firewood, and large quantities are shipped to Honolulu.

The prime value of the native forest is as a watershed; protecting the steep mountain slopes and ridges from erosion by the torrential rains, and conserving the water supply. Large areas on all the islands are now included in the government forest reserves, under the control of the Territorial Bureau of Agriculture and Forestry. These reserves are being extended from year to year. The fencing of the reserves to keep out cattle; the enforcement of trespass laws; and the extermination of the

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ubiquitous and highly destructive wild goats and cattle, are prominent features in the preservation of Hawaii's beautiful native forests. The forest is unusually susceptible to injury and deterioration, and any harm to it irreparably affects the rich undergrowth as well. There are few places in the world where the imperative necessity of forest conservation is as strikingly demonstrated as in the forested mountains of the Hawaiian Islands.

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BOOKS AND CURRENT LITERATURE

REVEGETATION OF RANGE LANDS.—This paper[1] presents the results of the application of ecological methods to the problem of range management and deals with many of the most interesting and important phases of plant ecology.

The investigations were carried on from 1907 to 1910, inclusive, in the Wallowa Mountains of northeastern Oregon, under the direction of the Forest Service and the Bureau of Plant Industry. Unrestricted grazing had brought about a decrease in the carrying capacity of the range due to early grazing, trampling and overstocking. The purpose of the investigation was to determine the best means of revegetation and the maintenance of a high degree of plant production without at the same time reducing the returns to the stockman. By a carefully planned series of permanent quadrats the author was able to determine the life history of each of the more important plant species of the range. The effects of different methods of grazing and of the varying conditions for growth were clearly ascertained. With this as a basis of judgment, a number of practical methods of grazing were tested. The results of the ecological study were applied to the practical problems of the range. It was possible from the investigations to manage grazing land in such a way as to produce not only the maximum amount of forage each year but at the same time to maintain the highest degree of efficiency over an indefinite period.

The area under consideration when divided into climatic zones on the basis of Merriam's "Life Zones," falls into four principal groups:

The Transition Zone	3000–4500 feet elevation
The Canadian Zone	4500–6800 feet elevation
The Hudsonian Zone	6500–8500 feet elevation
The Arctic-Alpine Zone	above 8000 feet

The principal plant associations represented in each of these zones are respectively the Yellow Pine, the Lodgepole Pine, the White Bark

[1] Sampson, Arthur W., Natural revegetation of range lands based upon growth requirements and life history of the vegetation. Jour. Agr. Res. 3: 93–148, pls. 12–23, 6 figs., 1914.

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Pine and the Alpine meadow associations. The climatic conditions of the three lower zones are recorded. The maximum temperature in the Hudsonian zone in 1909 was 91° F.; in the Canadian, 97° F.; and in the transition zone, 105° F. These figures stand in about the same ratio as the temperature differences noted throughout the season. In the Hudsonian zone the precipitation amounts to about 17 inches and comes largely in spring, autumn and winter. This zone is well supplied with water and, except in the case of seedlings, plants do not suffer from drought. A higher evaporation rate was recorded in the Hudsonian than in the Canadian zone. The results, it is stated, are probably influenced by density of stand and it is not clear from the presentation that it was possible to give the evaporimeters equal exposures. In general, the conditions in the Hudsonian zone are more favorable to forage production than in the lower zones, owing to the lower temperature and heavier precipitation. Growth begins the last week in June in the Hudsonian zone, about five weeks later than in the Canadian and seven weeks later than in the Transition zone. The resumption of growth in the same zone and at the same level varied from 3 to 9 days due to slope, etc.

Most of the grazing land occurs within the area characterized by the White Bark Pine association. The trees occur in small dense clumps and the forage grasses occupy the larger intervening area. Of the grasses, the mountain bunch-grass, *Festuca viridula*, is by far the most desirable and most abundant. Although not so distinguished in the text, there are here two distinct associations, the White Bark Pine association, which alternates sharply with an association composed largely of mountain bunch-grass.

The life history, including the period of growth, time of seed production and seedling growth of each of the more important forage species, is then presented. Even under the most favorable conditions seedling production in the more desirable species is low. Undergrazing conditions, low plant vigor, and the correlated late growth result in decreased seed production and lessened seed vitality and, consequently, in a greatly reduced stand of seedlings. Plants which are deprived of their foliage early in the season do not reproduce. Seedlings develop rapidly, but many are lost during the spring following seeding. During the dormant period few seedlings are lost except by erosion.

Extensive quadrat records of areas grazed continuously, protected continuously, and grazed after the seed had been formed show that

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deferred grazing restores and maintains the vegetation without the loss of the forage crop. Since it prevents the accumulation of a large amount of dry forage it at the same time lessens chances of fire. Quadrats cropped at frequent intervals, compared with others cropped only after seed production, would have further emphasized the advantages of this system, since frequent cropping greatly reduces yield. In the Wallowa Mountains one-fifth of the grazing season remains after seed production and one-fifth of the land may be retained for deferred grazing. It is desirable to practice delayed grazing for at least two years in succession on each area in order to secure the best results.

The plant ecologist will find in this paper an excellent example of the practical application of ecological methods to the problem of range economy and will be amply repaid for a close inspection of the life history studies. The range man will find suggestions of practical value and applicable with minor modifications to all regions in which there is danger of depletion of the natural range.—H. L. SHANTZ.

PHYSIOLOGICAL BALANCE IN NUTRIENT MEDIA.—The method of water cultures has but recently been given attention with respect to the control of the several factors involved, a consideration which will be necessary to render the results obtained from it of far reaching physiological importance to the subject of plant nutrition. Shive[1] has recently made a distinct contribution to the development of this method.

The purpose of the investigation, as explained by the author, was to develop a nutrient solution, as simple as possible, which should be suitable for a control in future work with water cultures. By omitting potassium nitrate from the salts employed in Knop's nutrient solution there was obtained a new solution that retains all of the constituent ions of the original. The three remaining salts ($Ca(NO_3)_2$, $MgSO_4$ and KH_2PO_4) were employed by Shive in various different proportions and in three different total concentrations, the latter being sub-optimal, optimal, and supra-optimal with respect to the growth of young wheat plants. These three concentrations had total osmotic pressures of 0.10, 1.75 and 4.00 atmospheres respectively, and the partial pressure due to each salt was varied by increments of one-tenth of the total pres-

[1] Shive, J. W. A study of physiological balance in nutrient media. Physiol. Res., 1: 327–397. 1915. 15 figures.

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sure, by a method similar to that employed in the earlier work of the reviewer.[2] Thirty-six cultures thus constituted a series for each of the three concentrations. Data of yields and physiological disturbances apparent to the eye have been analyzed by Shive in considerable detail and the results are well summarized in graphic form. There is no doubt that Shive's best three-salt solution is eminently suited to serve as a present criterion of efficiency for nutrient solutions employed with the optimal concentration with which he worked, in the case of wheat. Data of yields from a number of solutions described in the literature and used by him simultaneously and at a uniform concentration establish this fact.

Among the several conclusions derived from this investigation the most important relate to the physiological balance of the constituent ions. The most significant is to the effect that the value of a given ratio of salts varies with the total osmotic pressure, or salt concentration, of the solution. A serious attempt to analyze in detail the ionic ratios involved in the many solutions employed developed the further conclusion that no single ratio of ions determines the effect of a given ratio of salts, but that the effect depends upon the interbalance of all the ions present. Attention is thus directed emphatically to the importance of considering the serious disturbance of physiological efficiency which may result whenever an additional chemical element, or ion, is added to any given nutrient solution.

In an effort to subject all the cultures of a series to uniform aerial environmental conditions to the fullest possible extent they were supported upon constantly rotating tables. Further data are given which support previous investigations with respect to a direct relation between transpiration and growth of wheat and an inverse relation between both transpiration and water requirement on the one hand and total concentration of the nutrient solution upon the other hand.

It is no small task to digest and summarize such a complex of data as have been treated in Shive's paper. The author is to be especially commended for the helpful methods of tabulation and illustration which he has employed. The field covered by the investigation is one of prime interest to physiologists on account of the great importance of the relation of soil nutrients to plant growth. The method here employed should lead to further experimental control and analysis of the

[2] Tottingham, William E. A quantitative chemical and physiological study of nutrient solutions for plant cultures. Physiol. Res. 1: 133–245. 1914.

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several factors involved in this complex relationship. Further work along similar lines should lead ultimately to much broader generalizations regarding the salt requirements of plants and the specific effects of their constituent elements upon plant growth than now obtain.—W. E. TOTTINGHAM.

FLORA OF THE NORTHWEST COAST.—The rapidly growing list of western floras has been augmented by the recent appearance of Piper and Beattie's Flora,[1] covering portions of Washington and Oregon. Unlike the great majority of manuals this one is devoted to an area with natural boundaries on all sides save one—the north. It embraces the portions of Washington and Oregon which lie west of the Cascade Mountains, and it does not include the Rouge and Umpqua valleys in the latter state, where the flora is similar to that of northern California. The flora of this heavily forested region is perhaps unique in the fact that it possesses twenty-two species of coniferous trees and only a single oak (except at its extreme southern edge). The well known floristic poverty of coniferous forests, together with the fact that this manual covers a natural and coherent area, makes the total of 1617 listed species a surprisingly large number. This carefully elaborated and well produced manual will replace the older Flora by Thomas Howell, although it covers a slightly smaller area.—FORREST SHREVE.

[1] Piper, Charles V., and Beattie, R. Kent, Flora of the Northwest Coast. Pp. 418, 1915. Published by State College of Washington ($1.75).

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NOTES AND COMMENT

In connection with the San Diego meeting of the Pacific Division of the American Association, on August 8, 9, and 10, 1916, the biologists of the western and Pacific states will meet to organize The Western Society of Naturalists. This follows upon the action of the Executive Committee of the American Society of Naturalists in rejecting the proposed affiliation of the Biological Society of the Pacific as a western section.

Mr. Samuel N. Rhoads, of the Franklin Bookshop, Philadelphia, has reprinted a rare and little known work which is apparently the earliest publication dealing with American plants and written by an American. This is William Young's Catalogue D'Arbres, Arbustes et Plantes Herbacees D'Amerique, printed at Paris in 1783. Young was a practical gardener, collector of living plants for export, and a traveler through the southern states. His annotated list of some 400 species gives much better descriptions of the soil conditions under which the plants are found than do the most recent lists of American plants written by Americans.

The Forest Products Laboratory, at Madison, calls attention to the importance of the sanitary handling of lumber and the maintenance of sanitary conditions in lumber yards. The cause of their admonition is the frequent occurrence of the so-called house fungus (*Merulius lachrymans*) and other wood-destroying fungi in the lumber yards of the eastern states. Such infection is doubtless responsible for the decay of timber in buildings in the same localities through the agency of these fungi.

The American Geographical Society has issued a sumptuous four hundred page Memorial Volume of the Transcontinental Excursion of 1912. In addition to considerable historical matter relative to the excursion, the book contains papers by some twenty of the foreign participants, chiefly on features of American geography in which they were particularly interested.

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The present year has witnessed the appearance of Soil Science, a journal edited by Prof. Jacob G. Lipman and published by Rutgers College, New Brunswick, New Jersey. This monthly affords a much needed medium for the publication of papers in soil physics, soil chemistry and soil biology.

A new course will be offered during the summer quarter at the University of Chicago, dealing with the methods used in ecological work, particularly with respect to measurement of environmental factors and field experimentation. The course is in charge of Dr. George D. Fuller.

A bequest has been made the School of Forestry of Yale University with a view to the offering of work in tropical forestry. The organization of courses is now under way and it is expected that the new work will be inaugurated by July 1.

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The Plant World

A Magazine of General Botany

VOLUME 19
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JULY, 1916

CONTAINING

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THE FIXATION OF FREE NITROGEN BY CERTAIN FUNGI

CHARLES OSCAR CHAMBERS

Oklahoma Agricultural and Mechanical College, Stillwater, Oklahoma

The fact that contradictory results have appeared from time to time in regard to the possibility of the fixation of free nitrogen by a number of molds and higher fungi, together with the recent development of a new and more rapid method for nitrogen determination, has made it seem worth while to repeat some of the published experiments by a new and more exact method.

In its chemical aspects the method is that recently developed and published by Dr. Otto Folin of the Medical School of Harvard University. It was suggested to me by Dr. P. A. Shaffer of the Medical School of Washington University, as having possibilities for this type of work. The problem undertaken was suggested by Dr. B. M. Duggar of the Shaw School of Botany, who had, himself, made some investigations along this line by the older methods. The cultures were prepared at the School of Botany and analyzed at the chemical laboratory of the Medical School of Washington University.

Acknowledgments are due to the men who have lent me their aid and direction in the prosecution of this work: to Dr. Shaffer for his patience and assistance in making the analyses; to Dr. Duggar for his suggestion of the problem and direction in regard to growing the cultures; and to both for the use of their laboratories in which the work was performed.

It seems evident, or at least likely, that the great variation in results and especially in the superabundant gains reported by some investigators must be due to errors in distillation and titration by the Kjeldahl method. These are avoided by the Nesslerization and colorimetric features as employed in the Folin method, and render a higher degree of accuracy possible.

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Moreover, the method, which will be designated as the micro-method, is adapted to a very small amount of the sample, using large test-tubes for digestion in place of the special flasks employed in the Kjeldahl method. This makes it possible to digest the cultures of fungi in the tubes in which they were grown and thus avoid the possibility of loss by transfer from the culture flasks to digestion flasks, as usually practiced in the Kjeldahl method.

These features, together with others to be mentioned later, lend facility as well as accuracy to the micro-method and make it possible to handle a large number of cultures with convenience and speed, both matters of great importance in making determinations of this character. It is the successful adaptation and application of the above features of a new method to an old problem and a partial solution of the problem that seemed to justify a publication of the results and a description of the method at this time, although a more exhaustive and more exact test will be necessary to settle even a small part of so large a problem as the one here represented.

HISTORY AND DISCUSSION

In a separate table is given a tabulated list of the chief investigators on nitrogen-fixation by fungi, together with the results of their work on *Aspergillus niger*. This and *Penicillium glaucum* have been the chief fungi used for this kind of investigation as well as for the other problems of nutrition. For this reason *Aspergillus* is of special interest.

The earliest investigator of whom we have any record, and hence of historic interest, is Jodin[1] whose work was done before the Kjeldahl method was known and is therefore lacking in scientific value. He simply states that his fungus grew well on a medium containing no combined nitrogen, which from our own experience seems doubtful. Moreover, pure cultures were not available to Jodin. Details as to length of time and amounts of cultures are not given.

[1] Jodin, Du rôle physiologique de l'azote. Compt. Rend. **55**: 1862 (cited by Frank, B., in Lehrbuch der Botanik **1**: 376.)

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Berthelot[2] gives positive results on cultures of *Aspergillus niger*, stating that in a month 5 to 10 mgms. was fixed by a culture of 600 cc. or more exactly, 4 to 9 mgms. after allowing 2 mgms. for uninoculated controls.

The first systematic study of definite fungi seems to have been made by Puriewitsch[3] whose work was chiefly on the above mentioned organisms, though it seems that he was not quite certain as to the purity of his cultures. The amount of fixation reported by him is scarcely beyond the limits of experimental error, and for that reason are strongly criticized by Czapek[4] who was not able to detect the slightest particle of fixation in any of his numerous cultures of *Aspergillus niger*. Puriewitsch states that the amount of fixation found by him was proportional to the amount of carbohydrate furnished in the cultures but that it has no quantitative relation to the amount of growth or dry weight. Both of these statements seem a little strange until we meet his statement that after some search for stray nitrogen he found it in the sugar furnished to his medium, in which case it would seem necessary that the nitrogen would increase in a direct proportion with the amount of sugar furnished. We should not, however, be too critical as to the interpretation of this incident, as his analyses may have made proper allowance for this item. At any rate, his work must be looked upon as a very good beginning and a model for this kind of investigation.

The investigations of Saida[5] confirm the results of Puriewitsch, but supply nothing new of importance except that he gives

[2] Berthelot, M., Recherches nouvelles sur les microorganismes fixateurs de l'azote libre. Compt. Rend. **116**: 847. 1893.

[3] Puriewitsch, Ueber Stickstoffassimilation bei den Schimmelpilzen. Ber. d. deut. Bot. Ges. **13**: 342–345.

[4] Czapek, F., Zur Kentniss der Stickstoffversorgung und Eiweiss-bildung bei *Aspergillus niger*. Ber. d. deut. Bot. Ges. **19**: 130–139. 1901.

Czapek, F., Untersuchung über die Stickstoffgewinnung und Eiweiss-bildung der Schimmelpilze. Beitrage f. Chem. Physiol. und Pathol. **1**: 538–546 and **2**: 557–590. 1902.

Czapek, F., Biochem. der Pflanzen **2**: 125–144. 1905.

[5] Saida, K., Über die Assimilation des freien Stickstoffs durch Schimmelpilze. Ber. d. deut. Bot. Ges. **19**: 107–115. 1901.

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rather strikingly high results as compared with the latter and sets a high pace for his followers. With his name ends the list of earlier investigators.

It is to Ternetz[6] more than any other that we are indebted for a wealth of data and detailed description of methods in

TABLE 1

Early investigators and results reported by them

NAME OF AUTHOR	AGE OF CULTURE	AMOUNT IN SOLUTION	KIND OF CARBOHYDRATE	FORM OF N	INITIAL N	GAIN N	PER CENT OF GAIN
	days	*cc.*					
'93 Berthelot.....	30	600	1% acid tartaric	ammontartr.	26.65	7.35	27
'95, Purewietsch...	60	50	5% saccharose	NH_4NO_3	2.1	2.20	105
'01, Saida.....	75	50	17% cane sugar	NH_4Cl	7.39	1.78	25
Recent investigators and results reported by them							
'03, Remy.....		1000	2% dextrose			10.00	
'07, Ternetz.....	55	100	5% dextrose	contamination	0.88	3.33	378
'08, Froelich.....	39	100	5% dextrose	contamination	0.96	0.46	48
'08, Latham.....	6	50	5% cane sugar	NH_4NO_3	117.2	205.1	174
'11, Lipman.....	30	100	2% dextrose		2.45	2.35	91
Investigators who found negative results							
'91, Winogradsky							
'02, Czapek.....	21	50	3% dextrose	many kinds	various	0.00	00
'10, Dox.....							
'11, Duggar and K.			many kinds	many kinds			?
'04, Koch.....							
'11, Pennington ...		100	1% dextrose	contamination	0.56	0.09	00
'13, Chambers.....	30	5	2% dextrose	$(NH_4)_2SO_4$	1.00	0.00	00
					2.00	0.00	00

handling this type of work. While her work was chiefly on fungi of the mycorrhiza group yet she reports fixation by *Asper-*

[6] Ternetz, Ch., Die Assimilation des atmospharischen Stickstoffs durch einen torfbewohnenden Pilz. Ber. d. Deut. Bot. Ges. **22**: 264–272 and **44**: 1904. 353–485. 1907.

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gillus niger that confirms the results of the earlier investigators. She states that the amount of fixation by molds is so imperceptibly small as compared with that of bacteria as to throw doubt upon the reliability of the Kjeldahl method for making such determination with sufficient accuracy. Two of the six sources of error mentioned by her, as found in the use of this method are:

(1) inaccurate titrations (standardization) of $\frac{N}{10}$ solutions as commonly used in this method.

(2) lack of sharpness in color indicators. These two sources of error are largely eliminated by the colorimetric method.

The work and results of Latham[7] present the most striking puzzle; first in the enormous amount of fixation given in some cases, and secondly in the great variance in her figures, *e.g.*, from 44.9 to 193.6 mg. in 50 cc. of culture solution. Her statement that nitrogen is consumed by the fungus from the culture solution in proportion to stimulation, is the characteristic point in her work but does not seem to receive full explanation.

Lipman[8] is the most recent investigator to report fixation by *Aspergillus niger* and his results are far from small, but seem to be consistent. He has nothing special to say in regard to any special methods by which these large results are obtained.

When we turn to the list of those who have reported negatively on *Aspergillus niger* we are confronted by a dearth of data except in the work of Czapek already mentioned. His work was not directed specially toward the question of fixation but is limited to the simple statement that no fixation could be detected though diligently sought for.

From Winogradsky[9] we have very little more than the bare negative statement; but this statement, from so prominent an authority on this subject, together with that of Czapek must carry great weight.

[7] Latham, Marion E., Nitrogen assimilation of *Sterigmatocystis nigra* and the effect of chemical stimulation. Bull. Torr. Bot. Club **36**: 235–255. 1909.

[8] Lipman, Chas. R., Nitrogen fixation by yeasts and other fungi. Jour. Biol. Chem. **10**: 169–182. 1911–12.

[9] Fröhlich, H., Stickstoffbindung durch einige auf abgestorbenen Pflanzen häufige Hyphomyceten. Jahrb. f. Wiss. Bot. **45**: 256–302. 1908.

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The details of the work done by Duggar and Knudson[10] are not available but the general tone is toward the discredit of the results of Miss Latham.

The work of Pennington[11] though not yet exhaustive, being comparatively new, seems however to have been carefully done and merits much consideration. His first work was done upon *Aspergillus niger* and seems to have been stimulated by the apparently incredible gains shown in the reports of Miss Latham. As already mentioned he is one of the few to have employed the colorimetric method, and that only sparingly. His work was not known to me until near the end of my own. He has not in any sense made use of the micro-method.

The field seems to be open for workers and there are many gaps yet to be filled.

METHOD

The micro-method offered a number of perplexing and discouraging difficulties at the outset, most of which had to be met and solved anew, even though they were well known in the old method, as they had never before been tested in this connection. On this account it seemed best to follow at first the methods of the earlier investigators and still followed, so far as I am aware, by all the later ones.

Accordingly, I followed essentially the method of Puriewitsch[12] and Ternetz[13] both as to kinds of media and method of determination of nitrogen, checking by Kjeldahl, the theoretical amount of nitrogen furnished in the cultures and making determinations both before and after growth. But it was the unusual gains reported by Latham[14] which offered the strongest

[10] Duggar, B. M. and Knudson, L., Relation of certain fungi to nitrogen fixation, Science **31**: 191. Feb. 1911.

[11] Pennington, L. H., Upon the assimilation of atmospheric nitrogen by fungi. Bull Torr. Bot. Club **38**: 135–139.

Pennington, L. H., Can Fusaria assimilate free nitrogen? Proc. Mich. Acad. Sci. **10**: 50, 1908.

[12] Puriewitsch, *l. c.*

[13] Ternetz, *l. c.*

[14] Latham, *l. c.*

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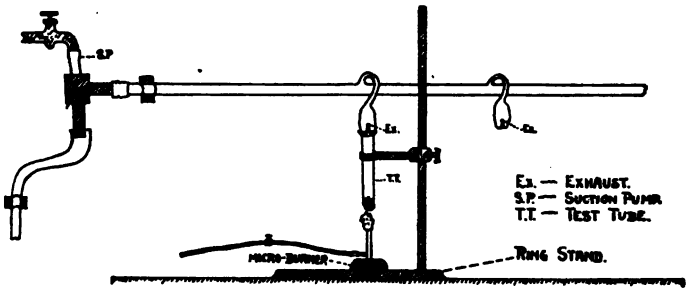
field of controversy and the methods of this investigator were kept especially in mind.

As is well known, but seldom mentioned by investigators, the carbohydrates used in the culture media cause serious difficulties in the Kjeldahl method and even more serious ones in the Folin method. These seemed at first to be insurmountable, for



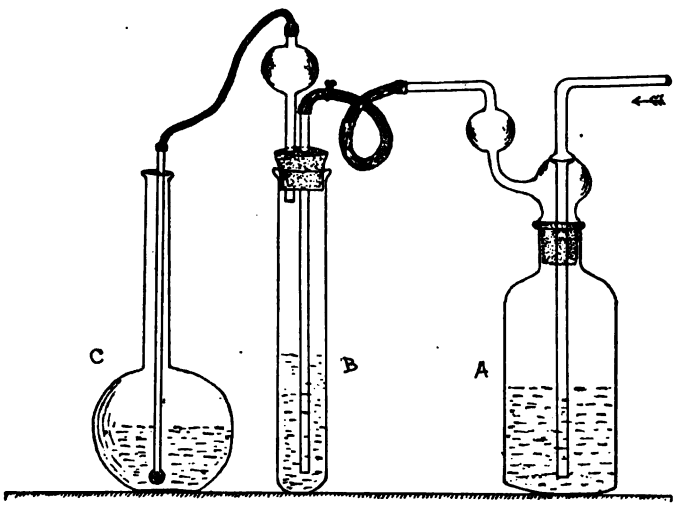


Fig. 1. After the sample has been digested in the test-tube, *t.t.*, in the upper figure, it takes the position *B*, in the detail figure below, where it is connected with the wash-bottle, *A*, and the receiving flask, *C*. A current of air from a compressor is admitted at the point indicated by the arrow and the ammonia is driven over from *A* into the receiver, *C*, where it is caught in a weak solution of hydrochloric acid and Nesslerized. The wash bottle *A* contains strong sulphuric acid to arrest any ammonia or other combined nitrogen that might be contained in the air current.

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the determination of the medium before growth. After growth, however, the carbohydrate has been transformed into forms that are more easily digested; and practice at length gave sufficient mastery of even the raw unseeded controls so that the Kjeldahl method was abandoned and the determinations were carried on by the micro-method exclusively.

The Folin, or micro-method, combines the essential features of the Kjeldahl and colorimetric methods reduced to micro-dimensions but with the special feature of blowing the ammonia over from the digestion tubes to the reception flasks and the values, read by a DeBoscq calorimeter. This seems to afford the highest degree of speed and accuracy when small amounts of nitrogen are to be determined. For details the reader is referred to the original sources as given by Folin.[15]

When sufficient accuracy had been attained by running a large number of blanks and checking by Kjeldahl determinations a number of *Aspergillus* cultures were prepared in large test-tubes (25 x 200 mm.) and allowed to grow for varying periods of time, from two to four weeks. They were then digested and determined by the micro-method. Cultures were grown in triplicates prepared as follows:

Dox's[16] nutrient solution was prepared with 2 to 3% dextrose and 5 cc. pipetted into each tube. To one set, A, was added 2 mg. of nitrogen in the form of $(NH_4)_2SO_4$; to another set, B, 1 mg., and to a third set, C, no nitrogen was added.

The solution of $(HN_4)_2SO_4$ had been carefully prepared from very pure stock and standardized; first by weight and then by volumetric method, taking a standard that would give 1 mg. of nitrogen per cubic centimeter of solution. This was further standardized by running samples through the Kjeldahl process and titrating against very accurately prepared solutions of

[15] Folin, O. and Farmer, C. J., A new method for the determination of total nitrogen in urine. Jour. of Biol. Chem. **11**: 493–501. 1912.

Folin, and Denis, W., An apparatus for the absorption of fumes. Jour. Biol. Chem. **11**: 503–505. 1912.

[16] Dox, A. W., The intracellular enzymes of *Penicillium* and *Aspergillus*. U. S. Bur. An. Ind. Bul. 120: 37. 1910.

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HCl and NaOH, the results of which agreed with the theoretical values.

This solution, prepared and standardized with the highest degree of care and accuracy, was pipetted into the separate culture-tubes by means of a special Ostwald pipette.

These culture solutions, thus prepared, were then sterilized in the autoclave at 15 to 17 lbs. pressure for 20 minutes and when cool they were inoculated with spores from newly grown *Aspergillus niger* and incubated at 28 to 30°C. for varying lengths of time, as shown in the tables, from 12 to 30 days.

TABLE 2

Experiment A. Aspergillus and Penicillium cultures in Saida's solution with 5% cane sugar and nitrogen as $(NH_4)_2SO_4$ added. 1 cc. and 2 cc, respectively, added to 5 cc. of solution = 6 and 7

AGE	NUMBER	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT GAIN
days		*°C.*				
30	1	21	1.00	1.00	0.00	00
30*	1	21	1.00	1.00	0.00	00
30	2	21	0.00	0.00	0.00	00

* The cultures of Penicillium gave the same results as Aspergillus. Both produced a good growth and abundant spores when nitrogen was furnished but when not furnished merely germinated and produced no further growth that could be called normal. The Penicillium was abandoned after this experiment. Saida's solution is made up as follows: K_2HPO_4 0.4 gm., $MgSO_4$ 0.4 gm., $CaCl_2$ trace, water 100.0 cc.

As controls, a set of similarly prepared solutions were inoculated just previous to sterilization and kept after sterilization, with the dead spores, alongside the other tubes throughout the remainder of the experiment and analyzed at the same time as the others. This was afterwards found to be unnecessary as the spores contained only a negligible amount of nitrogen and this method was abandoned for another simpler one.

It was agreed that the taking up of nitrogen from the air is simply a matter of absorption, governed by the laws of diffusion and since this is dependent solely on the amount of absorption surface presented by the culture, blanks of water only would serve the same purpose, cost less trouble to prepare, and be

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much easier to digest. Hence this kind of control was resorted to from Experiment D to the end. It was even considered useless to analyze these so long as there was no apparent gain in the cultures over that supplied.

At first, sets of cultures were kept under air-tight bell-jars and aerated by means of a suction pump, drawing the air first through wash bottles, one containing NaOH and the other containing H_2SO_4 to remove any combined nitrogen. This was later abandoned along with the controls, as already mentioned, and for the same reason.

It seemed quite significant that when the cultures were analyzed after 30 days that they would yield exactly as much nitrogen as had been put in at the beginning and no more, as shown in Experiments A, B, and C. This ratio, however, did not hold out, as will be seen by the remaining experiments.

The water-blank controls kept as above described showed no accumulation of nitrogen when analyzed. The blanks kept with dead spores gave some color when digested and Nesslerized but later, by the adoption of a special uniform method of inoculation this was reduced to a negligible quantity as detailed on a later page.

The live spores to which no nitrogen was supplied simply germinated and made a thin ghostlike mycelium but made no real growth and yielded only the same depth of coloration as the dead spores alone yielded. This confirms the statement of Dox that "Nitrogen in some combined form is essential, for the molds (*Aspergillus* and *Penecillium*) can not utilize atmospheric nitrogen sufficiently to produce a normal colony. Often a slight growth of mold had been observed in the absence of nitrogenous compounds, but this is to be regarded as due rather to the reserve protein present in the spore itself or to a small amount of nitrogenous substance transferred to the medium during inoculation.

This, according to the experiments and logic of Boussingault, should have been regarded as conclusive evidence against the possible fixation of free nitrogen by *Aspergillus niger*. However, my results do not agree with a number of investigators, including Puriewitsch and those in the tabulated list.

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Some of them report a considerable gain of nitrogen without any initial nitrogen furnished, which would imply a vigorous growth, although that point is seldom mentioned by any of them. Some, as Dox, mention the fact that there was no growth beyond germination.

It seemed that any further precaution in the way of controls and the exclusion of combined nitrogen from the atmosphere

TABLE 3

Experiment B. Aspergillus in Czapek's solution with 5% dextrose. In other respects the same as Experiment A, viz., 5 cc. of solution + 1 cc. or 2 cc. of ammonia solution per culture, making 6 cc. and 7 cc. respectively

AGE	NUMBER	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT GAIN	
days		°*C.*					
30	2	21	1.00	1.00	0.00	00	(a)
30	2	21	2.00	2.00	0.00	00	(b)
30	2	21	0.00	0.00	0.00	00	

Czapek's solution is made up as follows: K_2HSO_4 1.00 gm., $MgSO_4$ 0.50 gm., KCl 0.50 gm., $FeSO_4$ trace, water (dist.) 1000.00 cc.

TABLE 4

Experiment C. Aspergillus cultures in Czapek's solution with 5% dextrose. 5 cc. per culture + 1 cc. or 2 cc. of ammonia solution added, making 6 cc. or 7 cc. respectively, per tube

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	°*C.*	*mgms.*	*mgms.*	*mgms.*	
14	6	37	1.00	1.00	0.00	00
14	7	37	2.00	2.00	0.00	00
14	5	37	dead spores	0.00x	0.00x	00x

was unnecessary until there should be found some indication of a gain in nitrogen over that furnished at the outset, which had been measured with the greatest possible accuracy and without any apparent loophole or cause for doubt. In other words it was considered that it would be soon enough to look for the sources of fixation or gain and the relation to dry weight carbohydrate economy, etc., after some fixation or gain had been demonstrated and not before that.

Accordingly, cultures were continued as before, varying the

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media slightly and the temperature considerably, some being grown at room temperature, about 20°C. but mostly in the incubator at about 29°C. as this had been shown by Will,[17] Nitinsky[18] and Czapek[19] to be the optimum temperature for this organism.

The criticism might be made that the method failed to get all the nitrogen out of the cultures and that as a result no gain was shown; and this point calls for serious consideration. It is possible that the losses in D, E, G, and H are due to this cause; but Experiments A, B and C return exactly the amount of nitrogen that was supplied, and Experiment I, with *Azotobacter*, shows a liberal gain or fixation. The large loss shown in Experiment F, especially, was doubtless largely due to a change in the method of digestion, by adding a drop or two or H_2SO_4 and then evaporating until SO_2 fumes appeared. There is this feature in favor of the blowing-over method instead of distillation, and of the colorimeter method instead of titration, viz., there is less danger of driving over any of the alkali, which may occur in distillation. Even if this should occur it would have no evil effect, since the Nessler's solution to be added is itself strongly alkaline. For this reason there can be no error on the side of gain from this source, which by the distillation and titration method is possible. A slight increase in alkalinity from this source would be sufficient to cause the gain shown in some investigations reported. One such instance is cited by Pennington.[20] As to the process of digestion, it is the same in both methods. In both there is danger of contamination from the acid, which may contain ammonia. This occurred in one of my spore determinations showing a high amount of nitrogen, traced to a stray bottle of H_2SO_4 which had been left in the place of my tested acid.

[17] Will, H., Uber die Assimilation des atmospherischen Stickstoffs durch Pilze. Jahrb. f. wiss. Bot. **44**: 353–408. 1907.

Will, H., Beiträge zur Kentniss der Sprosspilze ohne Sporbildung, etc. Centrb. f. Bact., etc. **34**: 1–42, especially pp. 17–23. 1912.

[18] Nitinsky, Jacob, Uber die Beeinflussung der Entwickelung einiger Schimmelpilze durch ihre Stoffwechselproducte. Jahrb. f. wiss Bot. **40**: 1–93. 1904.

[19] Czapek, *l. c.*

[20] Pennington, *l. c.*

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The method used by myself had the special advantage that exactly the same standard was used throughout; *i.e.*, the same identical solution from which the supply of nitrogen was taken for the cultures, in the beginning, was used as the standard for Nesslerization at the end. No such rigid test or standard is possible in the titration method and ordinarily would not be observed in the colorimetric method.

TABLE 5

Experiment D. Aspergillus cultures in Czapek's solution containing 5% dextrose. Each culture containing 5 cc. of the solution, to which was added either 1 cc. or 2 cc. of the ammonia solution

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgms.*	*mgms.*	*mgms.*	
24	6	21	1.00	1.06	0.06	6
24	7	21	2.00	1.87	−0.13	−6

The blanks kept with this set were not analyzed since those kept and analyzed in the other experiments showed no gain and further because it was decided at this point to abandon the use of controls containing nutrient solution for reasons stated in the text.

TABLE 6

Experiment E. Aspergillus cultures in Czapek's solution with 2.5% sodium citrate and 2.5 dextrose. Each culture containing 5 cc. of the solution, to which was added 1 cc. or 2 cc. of the 1 mgm. ammonia solution

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgms.*	*mgms.*	*mgms.*	
24	11	33	1.00	0.99	−0.01	− 1
24	11	33	1.00	0.95	−0.05	− 5
24	12	33	2.00	1.60	−0.40	−20
24	12	33	2.00	1.60	−0.40	−20

In order to insure that the chemicals used, both in the culture and in the analyses, should be pure and free from nitrogen, except when its presence was desired, numerous blanks were run from the supplies.

The most likely source of error of this character would be in the carbohydrates furnished, as these are used in larger quantities than any of the other ingredients. Only the best brands

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of chemically pure stock were used, as they alone would be reliable.

It seems highly probable that some of the gains shown in the work of Puriewitsch were derived from his carbohydrates; in fact he admits that in the preliminary tests of his culture media the nitrogen was higher than it should be by theoretical calculations. He attributes the error to N-compounds in the sugar which he used. Consequently it would be expected that with increase of sugar there would be a proportional increase of apparent gain in nitrogen as given in his results. The same was true of Stahl[21] and of Fröhlich.[22]

In my work the amount of chemicals used, other than carbohydrates, was so small that the danger of contamination from the other chemicals was very small. Also, in the analysis by the micro-method such small amounts of chemicals are required that it is possible to keep them scrupulously tested and protected against contamination much more efficiently and easily than in the other methods.

Triply-distilled water was used in making culture solutions, after the first preliminary sets, and specially distilled water was used in all the analyses, having been shown by tests to be absolutely free from ammonia. The nitrogen supply furnished in the culture-media was taken in the ammonia form, ammonium sulphate $(NH_4)_2SO_4$, because it gave normal growth, as shown by Nitinsky[23] and Czapek.[24] Also, this form presented no difficulties in the digestion process such as would be met with in the use of nitrates.

Dextrose was finally adopted as the source of carbohydrate largely because it is stated by a number of investigators, including Czapek, Fröhlich, and Lipman to give the best growth with *Aspergillus*. The dextrose which I used bore the mark of Merck. The other chemicals bore the name of Baker and

[21] Stahel, G., Stickstoffbindung durch Pilze bei gleichzeitiger Ernährung mit gebundenen Stickstoff. Jahrb. f. wiss. Bot. **49**: 579–615. 1911. (See p. 599).

[22] Frölich, *l. c.*

[23] Nitinsky, *l. c.*, pp. 17 and 33.

[24] Czapek, *l. c.*, p. 138.

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Adamson. Where solutions were measured with a pipette, a special pipette was provided for each separate case or purpose and was never used for any other. The test tubes in which the cultures were grown and digested (both being the same) were first scrubbed then boiled with cleaning fluid, then allowed to stand 24 hours or more and again scrubbed out and rinsed with tap water and finally with distilled water. Jena tubes should have been provided for this purpose but unfortunately were not available and much loss and trouble resulted through breakage.

TABLE 7

Experiment F. Aspergillus cultures in Czapek's solution containing 2% dextrose. Each culture contained 5 cc. of the solution, to which was added 1 cc. or 2 cc. of the 1 mgm. ammonia solution

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgms.*	*mgms.*	*mgms.*	
30	6	29	1.00	0.63	−0.37	−37
30	6	29	1.00	0.71	−0.29	−29
30	6	29	1.00	0.71	−0.29	−29
Average of three				0.68	−0.31	−31
30	6	29	2.00	1.74	−0.26	−23
30	6	29	2.00	1.54	−0.46	−13
30	6	29	2.00	1.66	−0.34	−17
Average of three analyses				1.65	−0.35	−17

In the analysis of the above only 2 to 3 drops of H_2SO_4 were added to hold the ammonia while the mixture was evaporated until SO_2 fumes appeared; then the remainder of the chemicals was added and the digestion completed. This made the digestion much easier and reduced the time considerably but it may also have caused the loss of nitrogen.

Since the amount of material to be digested in these analyses was greater than that in the experiments described by Folin it seemed necessary to increase the amounts of chemicals and the length of time was necessarily increased, often requiring over an hour for completion. But with practice I found it possible to reduce the time to half an hour for digestion. It seemed best to increase the time for blowing over to fully twenty minutes or double the time taken in Folin's work. While I doubled the

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amount of acid, using 2 cc. instead of 1 cc. I found it best to use only 1 cc. of K_2SO_4 as a larger amount caused a heavy precipitate of K_2SO_4 on account of the larger amount of NaOH necessary to neutralize the 2 cc. of H_2SO_4. On this account, also, it was found necessary to use 10 cc. of water instead of 6 cc.

TABLE 8

Experiment G. Aspergillus cultures in Czapek's solution with 2% dextrose. Each culture contained 5 cc. of the culture solution, to which was added 1 cc. or 2 cc. of the 1 mgm. ammonia

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgms.*	*mgms.*	*mgms.*	
28	6	29	1.00	0.91	−0.09	−9
28	6	29	1.00	0.91	−0.09	9
28	6	29	1.00	0.93	−0.07	7
Average of three				0.916	−0.084	8.3
28	7	29	2.00	1.86	−0.14	7
28	7	29	2.00	1.64	−0.36	.18
28	7	29	2.00	1.82	−0.18	9
Average of three				1.77	−0.23	11.5

TABLE 9

Experiment H. Aspergillus cultures in Czapek's solution with 2% dextrose. Each culture contained only 5 cc. of the solution, the ammonia solution being included in the solution when it was made up, so that there was no dilution

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgm.*	*mgm.*	*mgm.*	
14	5	29	1.00	0.87	−0.13	−13
14	5	29	1.00	0.97	−0.03	3
Average of two				0.92	−0.08	8
14	5	29	2.00	1.84	−0.16	8
14	5	29	2.00	1.92	−0.08	4
14	5	29	2.00	2.00	0.00	0
14	5	29	2.00	1.94	−0.06	3
Average of four				1.925	−0.075	3.75

20 cultures were prepared. The others were lost through breakage or other accident.

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Certain minor difficulties can be learned and mastered only by experience and can not well be described in print. I learned by experience that it was fairly easy to manage the difficulty and annoyance caused by foaming. If the digestion is begun with acid and $CuSO_4$ only, and continued with a low flame until the foaming reaches the maximum, and the flame is then kept extremely low, the critical point in the foaming may be passed in less than one minute. Then the K_2SO_4 may be added a little at a time, when the foaming will diminish and nearly cease, and the flame may then be turned up to its maximum. The digestion will then go on to completion without further difficulty.

After the liquid becomes clear it is allowed to cool but not to solidify. Then 6 to 10 cc. of water is added, or enough to keep the liquid clear when the alkali is next added. A drop of indicator is now added. Three cc. of saturated NaOH will be sufficient to render the liquid alkaline. A good way to introduce the alkali is to suck it up into the blowing tube and to hold it there by means of a clamp until the rubber stopper is inserted in the test-tube and made air tight, then the clamp may be released. The current of air may now be turned on, slowly at first and increased towards the last to a maximum—as much as the apparatus will stand.

The ammonia is blown over into a 100 cc. volumetric flask which contains 20 cc. of water and 2 cc. of $\frac{N}{10}$ HCl. When the blowing is completed, which will require about twenty minutes, the volume may be made up to 50 cc. and the diluted Nessler's reagent (5 cc. plus 20 of water) may be added with such care as to prevent any clouding. A standard flask made up in the same manner and as nearly as possible at the same time, containing a standard amount of nitrogen; in my case always 1 mgm. of the standardized $(NH_4)_2SO_4$ is used as the standard of comparison for reading in the Duboscq colorimeter. It is well to discard 20 to 30 cc. of each from the top and use from the remainder. It is also well to wash the cups and glass prisms of the colorimeter with the solution to be tested before proceeding.

In my practice the standard was set at 20 on the colorimeter. The vernier reading on the other side, taken in inverse ratio gives the amount of nitrogen in milligrams.

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MODE OF INOCULATION

As a check on the amount of nitrogen carried in by the spores it was necessary to adopt some uniform method of inoculation and observe some precaution. The platinum wire was bent at a right angle, making a straight foot 3 to 4 mm. long. The point of this was first moistened by touching it to the solution in the tube to be inoculated, then touched to the mass of spores in the culture tube, taking only what would cling to the point. This was then touched to the surface of the nutrient solution, leaving only the smallest possible number of spores. After each inoculation the remaining spores were all burnt off the wire before the next inoculation.

A series of determinations on blank inoculations made in this same manner, and also in distilled water, in tap-waters showed that the amount of nitrogen was quite uniform and so small as to be negligible, less than 0.01 mgm.

Separate cultures were grown in small test tubes to determine whether any nitrites or nitrates were formed during the growth. These cultures were tested at the end of the period given to the regular cultures and were found not to contain any of the above compounds. The potassium iodide starch test was used for nitrites and the diphenylamine test for nitrates.

Blanks were run to test the effect of a larger or smaller amount of H_2SO_4 and K_2SO_4 used in digestion, and there was found to be no apparent difference. Bulletin 31 of the Bureau of Chemistry advises the use of double the usual amount of H_2SO_4 per K_2SO_4 to prevent foaming. Accordingly, I settled on 2 cc. and 1 gm. K_2SO_4 for each analysis. No nitrites or nitrates being found no modification of the digestion was thought necessary.

An unexpected source of error was discovered while testing some blanks supposed to contain no nitrogen, and at the same time some blanks freshly inoculated as described. Both were found to contain the same amount of nitrogen, namely about 0.1 mgm. A rigid search on a number of blanks showed that the 1 cc. of H_2SO_4 used in the digestion was its source. It was found that 1 cc. of the acid alone, put through the entire process

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of digestion, blown over and Nesslerized, gave the same color as when used with all the other substances.

In the above case the contamination was promptly discovered as due to a bottle of acid, left by someone in the place of the one which had been specially tested for this work. A new supply of acid which gave no color on Nesslerization was then used and

TABLE 10

Experiment I. Cultures of Azotobacter in Ashby's solution, containing 2% mannite and 0.05 mgm. of nitrogen as $(NH_4)_2SO_4$. Each tube contained 5 cc. of culture solution and 0.05 mgm. N.

AGE	SOLUTION	TEMPERATURE	INITIAL N	FINAL N	GAIN	PER CENT
days	*cc.*	*°C.*	*mgm.*	*mgm.*	*mgm.*	
7	5	29	0.05	0.10	0.05	100

Ashby's solution is made up as follows: Mannite 12 to 20 gm., Monopotassium phosphate 0.2 gm., Magnesium sulphate cryst. 0.2 gm., Sodium chloride 0.2 gm., Calcium sulphate 0.1 gm., Distilled water 1 liter. (Jour. Agric. Sci. 3: 38, 1907.)

The above figures show approximately the average of four analyses. For want of time they were not accurately measured but there was a liberal margin over the above gain. These are the only cultures of the entire nine sets that show a uniform and decisive gain. This gain, though relatively large (100%) is small when considered in terms of milligrams; but by the colorimetric method is quite decisive and beyond doubt as to the qualitative character of the result.

It should be noted in this connection that the above experiment is especially suited to show that the entire micro-method might be well adapted to this kind of work in general, where unusually small margins are to be taken into consideration. It has in it all the possibilities of speed, accuracy, and general convenience.

I have not seen, except in one or two cases, any mention of the colorimetric method used in this connection, and none as to such use of the micro-method. Pennington states that he made use of the color method in a few cases where very small amounts of nitrogen were to be measured and it has been used in the direct measurement of nitrites and nitrates.

the color given by the blank spore tests was considered so small as to be negligible, as already reported. It would be very necessary to guard against this source of error in either method. The HCl used in the receiving flasks should also be guarded and tested from time to time. There is less danger from the distilled water used, as the Nessler's solution is constantly diluted

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in it just before Nesslerization and any such contamination would always be detected.

It was found that there was sometimes a shortage, by failure to blow over all the ammonia known to be present. This is liable to occur if the digest is allowed to cool during the process of blowing and it may be found necessary to apply the flame.

SUMMARY

The strains of *Aspergillus niger* and *Penicillium glaucum* used in these experiments were not able to make normal growth on nutrient solutions when not furnished with combined nitrogen, although they were able to grow vigorously on the same solutions when furnished with combined nitrogen. This is taken to indicate that these organisms are not able to make use of free atmospheric nitrogen.

The chemical analyses indicate that *Aspergillus niger* does not fix free nitrogen.

The making of these analyses strongly indicates the adaptability of the Folin micro-method to work of this kind and to the analysis of cultures where very small amounts of nitrogen are to be determined.

NOTE:—Soon after the completion of this work an article appeared, describing an exhaustive study along similar lines, in which the author states that *Aspergillus niger*, among a number of other forms studied, shows no power of assimilating free atmospheric nitrogen. (Goddard, H. N., Can fungi living in agricultural soils assimilate free nitrogen? Bot. Gaz. **56**: 149–305, October, 1913.)

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THE DEVELOPMENT OF THE OVULE OF IMPATIENS PALLIDA NUTT.

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The genus *Impatiens* is represented chiefly in Asia, where in 1860 a collection of 100 species was made.[1] A much smaller number are natives of Europe, while only two species have been found in America. *Impatiens pallida,* Nutt. and *I. fulva,* Nutt. are abundant in moist localities in this region. Their range is from Quebec to Oregon, south to Georgia and Kansas. The former, *I. pallida,* is the species discussed in this paper. Except for the work of B. Longo[2] on the endosperm and the embryo, and of C. Brunotte[3] on the embryo, I have been able to find no record of researches into the life history of *Impatiens.* Their work was done on Asiatic and European species. This paper is an account of the development of the ovule of *I. pallida,* in which there are a few peculiarities.

The flowering season given for *I. pallida* is from July to September. This is true in respect to the ordinary fertile flowers, but the buds of the cleistogamous flowers appear late in May and last throuugh June. A few of them may even be found along with the flowers throughout the summer. These flowers resemble the ordinary buds externally but grow to a length of about 2 mm., the well developed stamens and pistil filling most of the space, the petals being aborted. After fertilization the capsule enlarges rapidly, pushing off the dry perianth. The average number and size of the seed produced by the cleistogamous flowers is the same as that produced by ordinary flowers, and so far as I have determined, the development is identical.

[1] Hofmeister, W., Allgemeine Morphologie der Gewachse. Leipsig 1868: 462.

[2] Longo, di B., Richerche su le *Impatiens.* Annali di Botanica. VIII: 5.

[3] Brunotte, C., Sur L' Ovortement de la racine principale chez una espèce du genre *Impatiens.* Comptes rendus, avril, 1896.

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Later in June yellow flowers appear which are like the ordinary open flowers except that they bear no stamens and pistils. At least this condition occurred in the plants studied in the summer of 1911. These sterile flowers persisted for only a short time, and before they had disappeared, early in July, the ordinary fertile flowers appeared. The first of October found the plants full of seed capsules in all stages, with still a few flowers among them. The flower is pale yellow, and those which I collected were not spotted. The mature seed capsule is about 2.5 cm. or 3 cm. long, and five-lobed, but very rarely contains more than three seeds. By the time the seeds are mature, the placenta is a mere thread extending through the length of the capsule.

DEVELOPMENT OF THE FLOWER

The development of the flower begins with the appearance of the saccate sepal, which covers the young bud like a cap throughout its development (fig. 1, A). Just within this sepal and the other two which closely follow it, a circle of small lobes indicate the beginning of the petals. Not until the petals have grown sufficiently long to over-arch the tip do the stamens begin to appear (fig. 1, B). The central space fails to show any sign of a pistil until the anther tissue is beginning to be differentiated, when a column arises from the flower axis (fig. 1, C). This column soon becomes dome-shaped and a section across it shows the five small cavities (fig. 1, F). When the pollen mother cells are beginning to form, the ovules begin to develop from the placenta (fig. 1, C).

THE OVULE

The ovules are produced on the axial placenta and arise in the usual way, forming at first a top-shaped protuberance. The archesporial cell does not appear before the protuberance is well started. It is probably a single cell of the hypodermis, though it is difficult to isolate, but the primary sporogenous and primary parietal cells appear clearly in the usual position (fig. 1, D and E).

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The primordia of the integuments, or at least the inner one, are present as soon as the ovule becomes distinct from the placenta, but their differentiation from the nucellus is not apparent until after the archesporial division. The average thickness of the integuments is about equal to that of the nucellus, which consists of five rows of cells. The ovule being anatropous, the outer integument is missing on the side next to the funiculus. Both integuments grow to equal length, and are prolonged far beyond the nucellus so that the embryo-sac lies near the center of the ovule (fig. 1, H).

Longo, in his paper on the Asiatic species of *Impatiens* refers to a large number of authorities, all of whom agree in the statement that *Impatiens* has two integuments. It is clear that *I. pallida* has two, and judging by Longo's figures, they are very similar in form to those of the species *I, amphorata*, but different from those of *I. roylei*. In the latter, the outer closes over the tip of the inner.

The innermost layer of the inner integument is composed of broad, flat cells forming a heavy tapetal jacket (fig. 1, I and J) similar to that which Chamberlain describes for *Aster novi-angliae*. As in the latter plant, these cells line the micropyle for a short distance, and are clearly a part of the integument. Such a jacket has been found in *Helosis*,[4] *Sium*, *Campanula*, in the Scrophulariaceae, and the Stylidaceae. It is evidently characteristic of the higher forms of Dicotyledons.

The nucellus consists of five straight rows of long slender cells with pointed ends, resembling tracheid cells (fig. 1, J). This phenomenon has been observed in a number of plants, *e.g.*, *Casuarina*, *Castania* and *Asclepias*, and is interpreted by Coulter and Chamberlain as suggesting a relic of their function as nutritive cells. The fact is more striking in *I. pallida* in that the chalazal cells immediately above the nucellus are of the same form, and a definite core of these cells may be distinctly seen and traced back until they join the tracheids in the funiculus (fig. 1, H).

[4] Coulter, J. M. and Chamberlain, C. J., Morphology of Angiosperms. New York, 1909.

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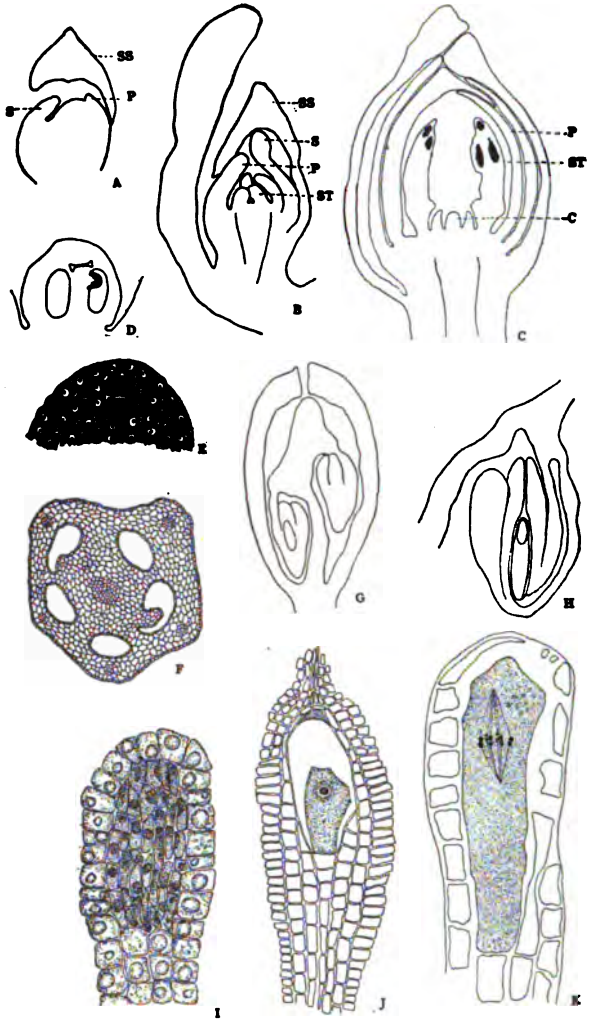

Fig. 1. A. Longitudinal section through a young bud; *S.S*, saccate sepal; *S*, sepal; *P*, petal. × 118. B. Older bud; further development of primordia. × 118. C. Bud with all primordia present; *p*, petal; *st*, stamen with anther tissue forming; *c*, carpels; *a*, appendages of the set of stamens behind those that appear in the figure. × 118. D. Longitudinal section of the ovary at the time of archesporial division (diagrammatic). E. Archesporial division has taken place. Primary parietal and primary sporogenous cells at the end of the axial row. × 530. F. A cross-section of the ovary at the same stage, showing the five cavities and ovules beginning to take the anatropous position (diagrammatic). G. Longitudinal section of the ovary showing the position of a fully formed ovule on the placenta (diagrammatic). H. A single ovule attached to the placenta, showing diagrammatically the apparent connection between the nucellus and the funiculus. I. The nucellus surrounded by the tapetum. × 530. J. The enlarging megaspore. × 530. K. The first division occurring in the embryo-sac. × 1000.

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Longo describes an abnormal development of the nucellus in *I. amphorata* and in *I. roylei*, in which the micropyle becomes filled during the development of the embryo, with a prolongation of the nucellus. In *I. amphorata* this prolongation extends beyond the mycropyle, and in *I. royeli*, it forms a large branching haustorium, penetrating deep into the tissue of the funiculus. In the haustorium the suspensor is imbedded. The outline drawings which accompanied Longo's paper did not make the nature of the haustorium clear in support of his statement, but for a number of reasons, I believe that they are not composed of nucellus cells. In the first place, there are no nucellus cells remaining in the micropylar end of the ovule in some of his drawings, and only a few fragments in others, at the time that the haustoria are developing. When the nucellus elongates, it is naturally during its active period, as in *Euphorbia corollata*[5] and not when it is disintegrating. Now the tissue in the drawing, in so far as its nature is shown, looks more like endosperm than like nucellar tissue, and it seemed that that was more likely its origin since there are many similar cases, *e.g.*, *Globularia cordifolia*, *Stylidium squamellosum*, *Biblis gigantia*, *Capsella bursa-pastoris*, and others. After reading Longo's paper, I made some slides of more advanced stages in my material and found a similar haustorium, though it was a short one, extending through from one-third to one-half the length of the micropyle. The tissue of this haustorium is clearly endosperm because (1) The nuclei are like the endosperm nuclei; (2) the staining is identical with that of the endosperm, and different from that of the nucellus; (3) the tissue is continuous with the endosperm. the drawings make the identity of the tissue clear (fig. 2, Q and S). There seems to be no question that the tissue in the micropyle of *I. amphorata* and of *I. roylei* is also endosperm.

There is no parietal tissue formed, a common condition among Archichlamydeae and universal among the Sympetalae.[6] Four megaspores are formed, the chalazal one developing at the expense of the other three (fig. 1, J). The nucleus divides as the

[5] Coulter and Chamberlain, *l. c.*
[6] Coulter and Chamberlain, *l. c.*

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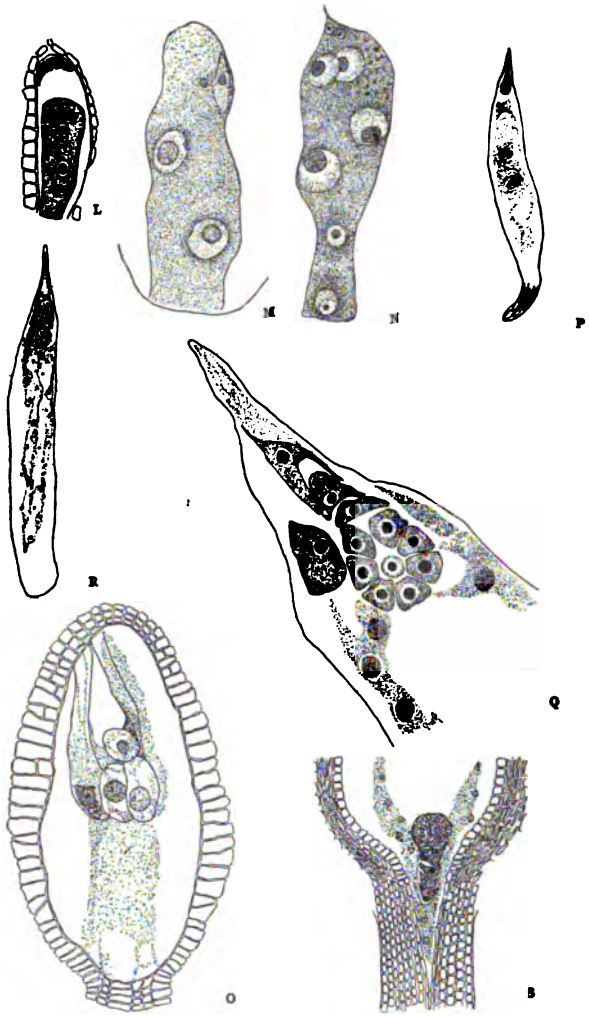

Fig. 2. L. A two-celled embryo-sac. × 530. M. A two-celled embryo-sac. × 1000. N. An eight-celled embryo-sac. × 530. O. A mature embryo-sac showing a pollen tube in contact with the egg, and apparently a second tube, or a branch in contact with a synergid. × 530. P. The fertilized egg just before division, and the polar nuclei. × 118. Q. The eight-celled embryo. × 530. R. The spherical embryo and endosperm. × 118. S. An embryo-sac showing the haustorium of endosperm tissue penetrating the micropyle. × 118.

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sac becomes larger and elongated (fig. 1, K), and subsequent divisions produce the usual eight nuclei. The antipodals cannot be distinguished with certainty, and are evidently transitory, as they are in *Euphorbia, Salix, Alyssum, Acer Habernaria, Casuarnia* and many others. The egg apparatus has a peculiar form, the egg being next to the micropyle and the synergids below it as in *Spirea japonica*. The egg is nearly spherical with a central nucleus, the synergids have the usual more or less oval form (fig. 2, O). The apparatus lies at some distance from the mycropyle. The fusion nucleus lies just below the embryo at the time of division (fig. 3, U). The polar nuclei did not appear in the sections with the egg apparatus represented in figures 2, O and P.

Just what occurs in fertilization is not clear. The pollen tube reaches a spot between the egg and one of the synergids, and a sperm nucleus may be seen in the tube, but the process could not be traced further. Fertilization probably takes place before the fusion of the polar nuclei. The peculiar structure which looks like a second pollen tube in contact with the synergid to the left (fig. 2, P) was not as distinct as the true tube represented in the figure, its clearness being somewhat exaggerated in the drawing. Its significance is not evident, but it suggests a possible branching of the pollen tube such as is found in some forms.

In the nuclear division which occurs in the embryo-sac the gametophyte number of chromosomes seems to be twelve. It is particularly clear in the first division (fig. 1, K).

The primary endosperm nucleus divides before the egg (fig. 2, P), the micropyle widens near the egg and a little of the cytoplasmic contents of the embryo-sac fill in the space. Thus the position of the haustorium is indicated before the suspensor is formed. The endosperm nucleus divides rapidly, forming a thick jacket around the developing embryo and lining the sac. The interior of the sac is nearly filled with endosperm when the embryo has reached the spherical stage. Several endosperm nuclei appear in the cytoplasm in the micropyle at this stage. The nature of the haustorium here becomes apparent. As the embryo develops the endosperm gradually disappears until it is entirely displaced. There is no endosperm in the seed.

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The embryo is formed by the division of the egg in the usual way. The suspensor is short and broad, and the cells are flattened as though they were under pressure (fig. 2, Q). It disappears almost completely by the time the embryo begins to elongate. The embryo retains its spherical shape after it is large and many-celled. Soon after it elongates a groove appears in the tip, and this deepens until the cotyledons are formed and the stem tip appears. By this time the dermatogen has become marked (fig. 3, V).

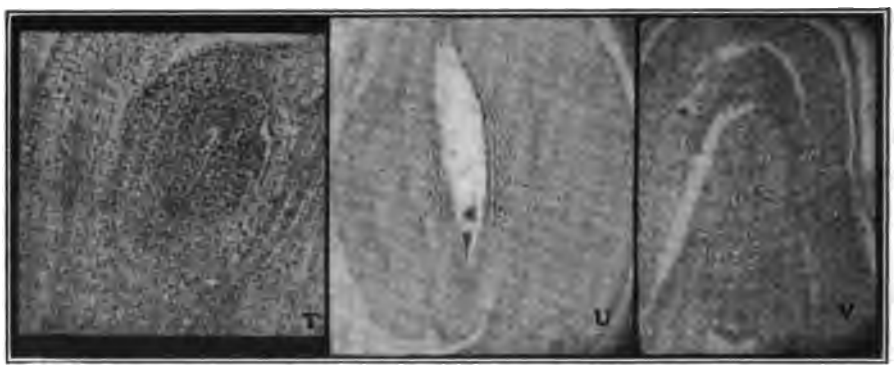

Fig. 3. T. Microphotograph of the first division occurring in the embryo-sac. *U*, Microphotograph of the fertilized egg just before division, with polar nuclei. *V*, Microphotograph of the base of an embryo, showing cotyledons and dermatogen.

During the growth of the embryo, first the nucellus, then the endosperm cells are used and then the inner integument begins to disintegrate to furnish food for the embryo. This proceeds in the integument from the outside inward. Finally, only the tapetal jacket and the beak-like end of the inner integument remain, the outer becoming thick and forming the only covering for the seed.

SUMMARY

The ovule of *I. pallida* has two integuments, the innermost layer of the inner one being composed of tapetum-like cells which persist after the integument has been resorbed. The cells of the

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nucellus are tracheid-like and meet a group of similar cells in the funiculus. Of the four axial megaspores, the chalazal one develops at the expense of the other three. The gametophyte number of chromosomes is probably twelve. The egg-apparatus is unusual in that the egg lies below the synergids. The antipodals are very transitory. The endosperm, which nearly fills the sac, produces an haustorial protuberance into the micropyle which first appears when the endosperm begins to be formed. Longo interprets a similar structure in *Impatiens amphorata* and *I. roylei* as nucellar tissue, but there is good evidence that it is endosperm. The endosperm is displaced by the developing embryo.

TECHNIQUE

The material was fixed in several different lots, corrosive sublimate solution being used for some, chromic-acetic acid solution for some, and a weak chromic-acetic with osmic acid for still others. The slides were cleared with xylol and mounted in balsam.

The most successful stain for the meristematic tissue was Delafield's Haematoxylin, and it was best when it followed corrosive sublimate fixing solution. For mitotic stages Heidenhain's Iron-alum Haematoxylin was used, usually in combination with Orange G., safranin gave good results as a stain for embryo-sacs.

All of the figures except D, F, G, and H were made with the camera lucida.

This paper is the result of work done under the direction of Prof. H. M. Benedict, to whom the author is indebted for help and suggestions. Thanks are also due to the Lloyd Library and to the Librarians for the use of literature.

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BOOKS AND CURRENT LITERATURE

RESPONSE IN DIONAEA AND DROSERA.—Two recent papers, one by Brown[1] and the other by Hooker[2] deal with the physiology of movement in leaves of *Dionæa* and in tentacles of *Drosera*.

Brown finds that *Dionæa* leaves grow at an increased rate during the reaction to a stimulus, the enlargement of the lower surface during closure and that of the upper surface during opening soon becoming permanent. Whether a leaf may close without permanently enlarging is not considered in this paper, although the measurements seem to show that enlargement becomes less during successive reactions. This may suggest either that the permanent enlargement is purely incidental or, more probably, that the active tissue is capable of but few responses. The percentage of increase in width of the lower surface was found to be 13.0, 9.0, 3.2, for three apparently successive closures of the same leaf.

The statement that enlargement occasions the movement in *Dionæa* affords an exception to the apparently almost general rule that response to shock stimuli is accomplished by a contraction of the motor tissue as a whole. However, it may be found that the accelerated metabolic activity of carnivorous plants during reaction, as shown by the formation and secretion of proteolytic enzymes and the like, may give rise to an accelerated growth rate. Hooker's observation, that *Drosera* tentacles retain their curvature when plasmolyzed soon after movement has been completed (see following review), may support this supposition.

Perhaps the most striking feature of Brown's paper is his treatment of the processes preceding the condition of permanent enlargement, so often loosely summed up in papers on similar subjects as "growth changes." He considers three groups of changes, one or more of which may possibly occasion the movement. (1) A sudden increase in the turgor of the motor cells may cause stretching of the

[1] Brown, William H., The mechanism of movement and the duration of the effect of stimulation in the leaves of Dionaea. Am. Jour. Bot. **3**: 68–90. 1916.

[2] Hooker, Henry D., Jr., Physiological observations on Drosera Rotundifolia. Bull. Torrey Bot. Club **43**: 1–27. 1916.

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cell walls and lead to permanent enlargement, without preliminary changes in the walls themselves. (2) The turgor may remain unaltered but the extensibility of the walls may increase. (3) The turgor of the ehlarging cells may remain constant while that of the opposing cells near the opposite surface of the leaf may decrease. The second possibility is dismissed by Brown as improbable, but it should be remarked that changes in cell walls have not received much attention and that such changes may be more important than they have appeared to be. The author concludes that his first possibility is the most probable, stating that the third alone cannot explain an adequate water movement into the expanding cells from those with lowered turgor. If the elastic cell walls of the enlarging tissue are stretched by increased turgor and if the metabolic processes that render the enlargement permanent become active only somewhat later, it might be expected that leaves killed just after closure would reopen if the water in them were replaced by some liquid in which the osmotically active material is insoluble. Following this suggestion Brown killed leaves in boiling water, transferred them to alcohol and then to xylene and found that they reopened. Since sugars are practically insoluble in xylene he concludes that they are of prime importance in producing the increased osmotic activity of these cells when closure occurs. Leaves that had been closed for some time, during which the permanent alterations of the cell walls may be supposed to have occurred, did not reopen in xylene.

This rather remarkable experiment, which was also performed successfully on *Mimosa*, should stimulate a more exact inquiry into the details of its interpretation. Since cane sugar and glucose are only slightly soluble in cold alcohol of sufficiently high concentration for this experiment, the leaves ought to open in alcohol if these are the sugars concerned. Maltose is more soluble in alcohol, however, and might act as Brown supposes. The question of the source of the sugar producing the increased concentration is also of interest, if we assume with Brown that an increased sugar content is the cause of the expansion of the cells near the ventral surface of the *Dionæa* leaf. The author states that starch is never found in these cells of irritable leaves and that some time after closure it becomes very abundant in the cells of the dorsal portion.

The location and nature of the membranes that are differentially active after the death of the tissues in this xylene experiment are of great general interest. If the protoplasmic membrane may thus func-

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tion after death, many current conceptions seem to require revision. If the cell wall proves to be effective in this case, as it appears to be in some seeds, inquiry into the precise character of cell walls which may thus act differentially would be of value.

On the other hand it is possible that Brown's xylene experiment may not deal with the actual mechanism of the living leaf, but may be concerned wholly with imbibition changes, in which a heavy-walled tissue shrinks more than an opposing thin-walled tissue, upon being transferred from a liquid that promotes swelling of cell walls (water) to one in which there is little swelling (xylene). Such tissues are present in *Dionæa* leaves and in the pulvini of *Mimosa* and occupy positions which might suggest such explanation.

Speculations such as these indicate the diversity of the problems presented by this paper and, while it is true that even the main features of the mechanics of the reaction in *Dionæa* can not be considered as settled as yet, Brown's work ought to stimulate investigation and it surely indicates some of the main lines along which further study may be profitable.

The second part of the paper deals with the relation between the frequency of equal, mechanical stimuli and the total time elapsing before the beginning and the end of leaf-closure. The results are expressed in the form of a graph which indicates that when the stimuli are applied at short intervals the number needed before closure is complete is relatively greater than when they are applied less frequently.

Hooker's paper on the tentacles of *Drosera* also records permanent enlargement of the active tissue during response, one side elongating during bending and the opposite side during recovery. The reaction may be repeated if a day without stimulation intervenes, but no more than three reactions could be evoked from the same tentacle. It is apparent from Brown's data that the same cells do not share equally in the successive reactions of *Dionæa*, and Hooker finds that the same portion of the tentacle does not respond in subsequent reactions. *Drosera* tentacles remained curved after plasmolysis had occurred and the permanent alteration of their cell walls is thus apparently accomplished more quickly in this case than in that of *Dionæa*, although there is nothing to indicate that the series of processes in the former may not include the intermediate stage observed by Brown. It is surely time that the various processes generally included under the term "growth" should be considered separately and that this word be no longer used to indicate a single "vital process." The two papers here reviewed

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stimulate speculation in the changes undergone by the cell walls during temporary and permanent enlargement of the cells, and it is to be hoped that they will also stimulate investigation on the same subject. Almost nothing is known of the chemical and physical properties of the cell wall and the alterations occurring in these properties under the influence of environmental conditions. The relatively great rapidity with which the walls must be altered during reactions like those of *Drosera* and *Dionæa* may render these plants suitable experimental subjects for certain phases of these problems.

In the case of *Drosera* the rate of transpiration appears to control its habit to a large extent, the low rosette appearing only with a relatively dry aerial environment. Prolonged high humidity is followed by more extensive elongation of the stem, the development of smaller leaves and by the loss of the red color. That a diminished transpiration rate is directly responsible for all these changes is not maintained by the author, for light and temperature were also altered when the air-humidity was raised. Lack of animal food produces a disappearance of the red pigment which may reappear within two days after the plant is supplied with insects.—H. E. PULLING.

DISEASES OF CULTIVATED PLANTS.—There has recently appeared a second edition of Massee's Diseases of Cultivated Plants and Trees,[1] which differs from the first edition published five years before only in the addition of a sixteen page supplement. This supplement contains accounts of diseases not included in the main body of the text, together with more recently acquired facts relative to the nature of certain diseases.

No name is so universally familiar in mycological literature as that of the author and probably no one has succeeded in bringing together so large a compilation of mycological facts as he. The present volume finds its most useful purpose in its vast assemblage of data, which makes it serviceable as a general reference work. The wide scope of the book can be known from the fact that consideration is given in the first eighty-seven pages to such subjects as epidemics, infection, dissemination, injuries brought about by drought, frost, hail, smoke, gas, etc., fasciation, bacteriology of the soil, fungicides, spraying, phanerogamic parasites, and the nature of fungi. The remainder of the book deals with plant diseases in Great Britain, Continental Europe, together with certain of those in the tropics and the United States caused by fungi,

[1] Massee, G., Diseases of Cultivated Plants and Trees. Pp. 618, figs. 173. The Macmillan Company, 1915.

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bacteria, lichens, slime molds, mites, eel worms and certain animals. In general, a brief descriptive characterization is made of each disease. This is followed by the most salient features of the causal organism and is concluded with brief suggestions for control.

Approximately two-thirds of the book is devoted to the fungi which produce diseases. The order of arrangement of these diseases is based on the systematic position of the causal organism. This arrangement, as is well known, has been followed by practically all of the authors of text-books of plant diseases. The writer is well aware, too, that in many colleges and universities, the presentation of the subject matter of plant pathology to students, centers around the causal organism rather than the resultant disease. In defense of this arrangement, attention is directed to the usefulness of an imaginary text book on "Diseases of Domestic and Feral Animals," constructed with the same ground plan.

While the proper arrangement of subject matter is largely a matter of personal opinion, it is regretted that the author has not seen fit to revise and bring up to date the body of the text, properly incorporate the supplement in the body of the text, remove a considerable number of inaccuracies and include the methods of control which have been devised and demonstrated during the past decade. This would have added very materially to the usefulness of the book both to the one who is interested in the fungi that cause plant diseases and the one who wishes to know of the plant diseases that are caused by fungi.

While no attempt will be made to list inaccuracies, several diseases have been noted which are described under the caption ascigerous stage and again under the conidial stage of the causal fungus. There is nothing to indicate a genetic connection between these stages, and the symptoms and control measures given differ. Certain organisms, too, are listed with one ascigerous state in one portion of the text and another on a succeeding page. Care should have eliminated these errors.

Consideration is given to an unusually large number of fungi, many of which are of importance to the mycologist only and are not productive of disease to economic plants. Rare diseases too are not infrequently given a considerable amount of space, whereas common, destructive maladies are confined to a single paragraph.

The book will serve a distinctly limited usefulness to the student of plant diseases in the United States since it covers so inadequately the American literature on plant pathology and since many important diseases find no mention in the book.—FREDERICK A. WOLF.

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NOTES AND COMMENT

During the past five years several new journals have appeared which are devoted to the various departments of botanical science. In spite of this fact it is not always possible for an author to secure prompt publication, particularly for a paper of more than 20 to 30 pages. It has been the custom of THE PLANT WORLD for several years to publish papers of undue length, or with numerous illustrations, only when the author was willing to meet a portion of the extra expense thus incurred. We are always ready to publish long or heavily illustrated papers, in their due turn, if payment is made for the number of pages in excess of 15 and the number of illustrations in excess of 4. Henceforth THE PLANT WORLD will also offer to give immediate publication (in 30 to 80 days) to any paper which is otherwise acceptable, regardless of its length, if payment is made for the total number of pages. The charge per page in either case is $2.75, the actual cost of such publication being about $3.75 per page for average matter. Papers published under this plan will be added to the regular contents of the issue and will be dated and specially designated. Papers in which more than 20% of the total space is taken up with illustrations, tabular matter and footnotes can not be considered under this arrangement. We hope to be able in this manner to assist the authors of extended contributions, both by offering prompt publication and by charging a rate per page which does not include the overhead expenses of this journal and does not include the entire cost of production—such rebate being given in recognition of the value of the longer papers to this journal.

A tract of about 600 acres of virgin pine timber was recently brought to light in southeastern New Hampshire by Prof. R. T. Fisher and Dr. I. W. Bailey, of the Bussey Institution. The whole aspect of this forest is said to be different from that of other old stands of timber in New England, and species of birds are to be found there which occur in virgin timber far removed from New Hampshire. Plans are being laid for a thorough biological study of this rare remnant of forest, and it is to be hoped that measures can also be taken for its absolute preservation.

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Prof. William Trelease, of the University of Illinois, announces the appearance of a monograph entitled The Genus Phoradendron. This is a complete reclassification of this group of mistletoes, and embraces descriptions of 240 species and 37 varieties, with half-tone illustrations of nearly all of the forms, nine-tenths of which have not been illustrated heretofore. The work may be secured from the Business Manager of the University of Illinois.

We have received the first number of Madroño, the new journal of the California Botanical Society, which is to appear at irregular intervals as a medium for contributions regarding the flora and vegetation of California and adjacent states, and as a chronicle of the activities of Californian botanists. Dr. W. L. Jepson, of the University of California, is chairman of the publication committee of the Society.

Professor Hugh Findlay, of the Slocum College of Agriculture, Syracuse, has written a useful popular book entitled House Plants, Their Care and Culture (D. Appleton & Company). The management of conservatories and window gardens, the preparation of soil, potting and propagation of plants, and the treatment of common diseases are all described, and brief directions are given for the care of the most frequently grown ornamental plants.

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PLANT SUCCESSIONS IN THE MOUNT ROBSON REGION, BRITISH COLUMBIA

WILLIAM S. COOPER

University of Minnesota, Minneapolis, Minn.

The observations here recorded were made during a brief visit to the vicinity of Mt. Robson, British Columbia, in the summer of 1914. The incompleteness of the study is thoroughly realized, and the only justification of this somewhat lengthy report lies in the fact that the region is absolutely new so far as ecological study is concerned. It may well be that many years will pass before a more thorough study is made. It is necessary also to explain that most of the plants collected for determination disappeared during a recent transcontinental journey, and for this reason many important plant names are of necessity missing or uncertain. With these apologies the author proceeds to make the best possible use of the data at his command.

Location. Mt. Robson is situated just upon the eastern edge of British Columbia, overlooking the Continental Divide, which at Robson Pass separates the Pacific from the Arctic drainage. Although the mountain is but six miles from the tracks of the Grand Trunk Pacific and Canadian Northern Railroads, it is almost upon the northern edge of the known country. Beyond it lie hundreds of miles of mountains as yet unmapped, and hardly even penetrated.

From the Robson Glacier, which descends from the north side of Mt. Robson to Robson Pass, the drainage flows toward both slopes of the Divide (or did so in the summer of 1914)—northward into the Smoky and finally into the Mackenzie and the Arctic Ocean, and southward into the Fraser and the Pacific, by far the greater bulk taking the latter course.

Topography. The relief in these mountains is very great. Slopes of six to seven thousand feet are frequent, and the south-

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west face of Mt. Robson, from its summit (13,068 feet, 4021 meters) to Lake Kinney (3250 feet, 1000 meters) is a single slope of 9800 feet (3015 meters), with an average inclination of 45°. The effects of present and past glaciation and of post-glacial weathering are of course apparent everywhere, and these are the controlling physiographic factors in reference to vegetation.

Climate. I know of no climatic records pertaining to this vicinity. It may be safely stated that precipitation is heavy and well distributed through the year. Cloudy weather with frequent showers is the rule in summer in the vicinity of Mt. Robson, but thunderstorms are rare. Upon Robson Pass summer temperatures are low, and frosts occur in midsummer, while upon the higher mountains snow falls in considerable quantities at frequent intervals. In the lower valleys the temperatures are considerably higher. At the main Fraser River (3000 feet, 923 meters) a temperature of 84°F. (30°C.) in the shade was noted July 4.

Vegetation zones. The vegetational and presumably climatic zones are three. The lowest extends in this vicinity up the Fraser and its Grand Fork to the cliffs at the head of Lake Kinney (3250 feet, 100 meters). The forest in this, which may be termed the Montane Zone, is of the type found upon the British Columbia Coast Ranges and in the lower zone of the Selkirks. In the region from 3500 feet (1077 meters) to timberline at 6500 feet (2000 meters)—the Subalpine Zone—the forest differs partially from the lower in species, and is very different in size of trees. Above timberline lies the Alpine Zone, characterized by Alpine meadows and rock and snow wastes. The present study deals with the two forest zones.

A. PHYSIOGRAPHY

Before discussing the vegetation it will be well to outline the physiographic processes which have been and are in operation in the region, since it is through the operation of such processes that new surfaces are laid bare for the initiation of primary

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successions. The agent of greatest importance is and has been ice. In the retreat of the glaciers since the time of their maximum extension fresh surfaces have been continually laid bare, and these surfaces have been mainly of two types: bare rock surfaces, largely cliffs; and moraines. Other physiographic agents began to act upon these surfaces as soon as they were exposed and to modify them profoundly. Thus we find the weathering processes engaged in the task of destroying the smooth rock surfaces. Temperature change, frost, solution by percolating water, and the mechanical and chemical action of plants result in the production of loose fragments of various sizes, which either remain in the spot where they were broken off or are carried to a lower level by gravity, according to the steepness of the slope. In the first case the layer of fragments first formed protects the surface from further extensive weathering; in the second case the removal of the products continually presents fresh surfaces. We thus find that the original rock surface, after a period of exposure, has generated a second type of surface; and there are now two types; areas that still remain bare and relatively smooth, or are kept so by the removal of the weathered material; and those that are covered by weathered fragments, either lying where they were split off, or else brought down from higher levels by gravity. The accumulations of the latter class, termed talus, are very extensive in the Mt. Robson region, as in all glaciated and recently glaciated mountains. The areas of loose fragments thus increase at the expense of the bare rock surfaces, which will finally be entirely eliminated.

Another agent, running water, is engaged in the destruction of the moraines. The streams issuing from the glaciers, already bearing much fine silt, remove these deposits, often with great rapidity, work them over, and finally deposit them, roughly sorted by sizes, at various places along their valleys, forming shingle and silt flats. Thus we see that the morainic areas also generate a second kind of surface, so that we find both uneroded moraines and shingle flats formed of materials derived mainly from them. The shingle flats are plainly increasing at the expense of the moraines.

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In these four primitive habitats: rock surface, fragmental accumulation (mainly talus), moraine, and shingle flat, four lines of succession originate, which we may term the Rock Surface Succession, the Talus Succession, the Moraine Succession, and the Shingle Flat Succession. All culminate in the establishment of a stable and permanent forest formation, the Climax Forest, which is the same for all the successions within a single climatic zone. It is not strange that in this locality the climax forests of the two zones are much alike, since here we find ourselves in the transition between the Rocky Mountain and Pacific Coast Forests. The forest of the Montane Zone is that of the Pacific coast; that of the Subalpine Zone belongs rather to the Rocky Mountain region. For the same reason the successions in the two zones are much alike, though with important differences in many details.

B. THE CLIMAX FORESTS

The Climax Forest in the Montane Zone is of the Pacific Coast type. It extends up the valley of the Fraser and up the Grand Fork to Lake Kinney. Much has been burned, but at one point between the mouth of the Grand Fork and Lake Kinney the trail passes through two miles of very typical British Columbia montane forest. A brief description of this will indicate the general character of the climax forest of the lower zone.

The most abundant tree is *Thuja plicata* D. Don. It attains a fairly large size, one being found which was two meters in diameter. Next in abundance is *Picea Engelmanni* Engelm.; and other tree species are *Abies lasiocarpa* Nutt., *Tsuga heterophylla* Sarg., and *Pseudotsuga mucronata* Sudw. Young tree growth is mainly *Abies* and *Thuja*. A shrub stratum includes *Acer glabrum* Torr., *Azaleastrum albiflorum* (Hook.) Rydb., *Menziesia ferruginea* Smith, and locally, *Fatsia horrida* (Sm.) B. & H. The herbaceous stratum includes, among many, *Phegopteris Dryopteris* (L.) Fee, *Equisetum sylvaticum* L., *Clintonia uniflora* (Schult.) Kunth, *Moneses uniflora* (L.) A. Gray, *Pyrola uliginosa* Torr. Mosses are abundant.

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Below this fine stretch of forest the country has been burned over for many miles, but relicts show that the original vegetation was like that described, doubtless becoming even more luxuriant down-riverward. Above, along the northeast shore of Lake Kinney, and upon the oldest parts of the shingle flat at its head, are areas of very similar forest, differing mainly in that the trees do not attain so large a size. The valley just above the shingle flat is interrupted by a "step" cliff, and beyond and above this the forest becomes that of the Subalpine Zone.

The Montane Zone is unfavorable for the study of successions, because of the almost total destruction of the primitive habitats, rock surfaces and moraines. The bulk of the territory is now divided between rocky and talus covered slopes and shingle flats. Vegetational development is correspondingly advanced. The climax forest makes an almost continuous cover upon the slopes, except where it has been destroyed by avalanche or fire, and successional stages are hard to find. On the shingle flats too there are tracts of mature climax forest, but areas in all stages of the succession are common here because of the continual erosional and depositional activity of the rivers. Bare rock surfaces are uncommon, and the moraines which formerly existed have been almost entirely destroyed. The successional stages related to these habitats are correspondingly incomplete in representation and difficult of observation.

The Climax Forest of the Subalpine Zone is poorer in number of species than that of the Montane, and two of its three species occur in the latter also. *Picea Engelmanni*, one of these two, which is of moderate importance in the lower forest, is greatly predominant here. *Abies lasiocarpa* is next in abundance, and *Pinus albicaulis* Engelm., absent in the Montane Zone, is present here, but was found nowhere in great abundance. The first species mentioned ordinarily makes perhaps nine tenths of the mature stand. Young growth is mostly *Abies*, which layers abundantly.[1] The following list of plants is sadly incomplete:

[1] Bot. Gaz. 52: 369–379; 1911.

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Menziesia ferruginea, Cassiope Mertensiana (Bong.) Don, *Moneses uniflora, Pyrola chlorantha* Sw., *P. uliginosa, Phyllodoce glanduliflora* (Hook.) Coville, *P. intermedia* (Hook.) Rydb., *P. empetriformis* (Smith) D. Don, *Cornus canadensis* L. Mosses are very abundant, the living plants and dead remains forming deep accumulations.

The difference between the forests of the two zones, particularly in regard to the larger woody species, consists rather in the elimination in the upper of certain species important in the lower, than in complete substitution of species. The absence of *Tsuga, Pseudotsuga, Thuja,* and *Fatsia* profoundly changes the aspect and character of the forest. This difference is an essential one too, since *Tsuga, Thuja,* and *Fatsia* are distinctively Pacific Coast species, while *Picea Engelmanni* and *Abies lasiocarpa,* dominating the Subalpine Zone, belong almost as distinctively to the Rocky Mountain region. In the lower growth conspicuous differences exist. The heaths, of little importance in the Montane Zone, are greatly predominant in the Subalpine; the mosses too are much more abundant in the latter.

For the study of succession, the Subalpine Zone is far more favorable than the Montane. In the former many of the glaciers reach their lower limits. None extend into the Montane. Since they are now in retreat, we find freshly exposed rock surfaces and moraines, and an abundance of talus slopes and shingle flats as well. In the vicinity of Robson Pass conditions were unfavorable for the study of the Rock Surface Succession, but there were easily available samples of the other three, in all stages of development. Most of the successional studies were made in the vicinity of Robson Pass and at Lake Kinney.

C. THE SUCCESSIONS

1. The Rock Surface Succession

Rock surfaces, mainly steep cliffs, are naturally common in the Mt. Robson region. Most of them are more or less unstable because of steepness and creviced condition, and are weathering

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rapidly, thus giving rise to large accumulations of talus at their bases, and continually exposing fresh surfaces above. Rock areas stable enough to allow the development of a rock surface succession were not studied, though without doubt they are abundant enough.

Studies in other regions have shown that two types of rock surface succession may be distinguished. (1) An area of slope slight enough to prevent removal of material by gravity may become covered by a layer of fragments, the products of its own weathering. Such will present conditions similar to talus, and vegetation upon it will develop along similar lines. (2.) If on account of smoothness and relative freedom from joints the rock resists weathering, vegetational development will be much slower, and will begin with lichens upon the smooth areas and crevice plants in the crevices, the lines of progress originating with these two sets of pioneers finally merging in a mat of vegetation resting upon the practically unweathered rock and anchored in the crevices. The latter is the common type of development upon the rock shores of Isle Royale, Lake Superior.[2] Doubtless both types could be found in the Mt. Robson region, but I have no observational data to offer. The process as suggested above must be regarded as hypothetical.

2. The Talus Succession

The observations upon which this account is based were made mainly in the vicinity of Lake Kinney; also near Emperor Falls. The normal course of plant succession is from lower plants to higher, both in size and in stage of evolutionary development. Thus a succession may be initiated by lichens or algae, and these will normally be followed by plants higher in the evolutionary scale and larger in size. In either case the final stage will be forest, climate permitting. In the talus succession, in the locality studied, the order is reversed, for the pioneers are trees, and the smaller and lower plants come at a late stage. The natural result of this anomaly is that the stages of the succession are

[2] Bot. Gaz. **55**: 115–140; 1913.

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poorly marked. There are no pre-forest stages, barring the sparse covering of lichens upon the fragments, which is of no consequence in the vegetational development. Two forest stages may be distinguished: the first, dominated by *Betula*

Fig. 1. Talus slope north of Lake Kinney. Birch-conifer forest with scanty undergrowth.

papyrifera Marsh, with occasional willows; the second by the climax conifers. Even these two stages are far from distinct, for certain of the conifers may enter apparently as early and as abundantly as the birches, the only reason why they do not at

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once attain dominance being that the breaking off of their trunks by falling fragments is always fatal to them. The birch, having met such a catastrophe, merely replaces its lost shoot with a cluster of stump sprouts, and so is helped rather than harmed by the disaster.

The tree seeds germinate in the crevices and cavities among the boulders—obviously the only situation where there is moisture, soil of any kind, and shelter. Possibly the reason why the climax conifers are able to establish themselves so early in so apparently forbidding a habitat is that the shade of the rocks performs the same service for them that the shade of the subclimax trees performs in the normal succession. By the time the shoots have emerged from the crevices the plants are well established. Herbaceous plants, especially those without the power of upward elongation, if they germinated, would be likely to die because of insufficient light, and they might easily be covered by debris from fresh falls of talus which might not harm well established woody plants. Of course this hypothetical explanation is to be applied only to the particular talus studied, in which the blocks are of medium size—from a few centimeters to several decimeters in diameter. If the fragments are very small and the mass is well consolidated, conditions are suitable for crevice- and mat-plants as pioneers, and the trees should appear later. With very coarse fragments the cavities would be so large and deep and the ground water so far from the surface that all invasion except by surface lichens would have to await further disintegration of the rock masses.

The trees and shrubs seen upon open talus were: *Betula papyrifera*, *Salix* spp., *Picea Engelmanni*, *Pseudotsuga mucronata*. Practically every tree upon open talus is scarred upon the upper side; many have large blocks resting against them. Broken trunks and branches are strewn over the slope. In some places rock falls are so frequent as greatly to retard the development of vegetation, or even to prevent it entirely.

As the birches become larger and more numerous they lessen the destructive force of the rolling and bounding talus blocks. More and more conifers escape destruction, and the forest

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comes to be a mixed conifer-birch aggregation. The elimination of the light-requiring birches and the complete dominance of the climax conifers is now a mere matter of time.

The development of the tree contingent may progress at least as far as the mixed birch-conifer condition before any considerable amount of lower growth appears. The establishment of the smaller plants awaits and depends upon that of the trees. Around, and largely below some of the willow bushes growing upon open talus were found small patches of humus and mosses, with occasional seedling conifers. Even in places where the birches and conifers were rather closely placed, the ground cover was little more extensive than this. Patches of *Arctostaphylos Uva-ursi* (L.) Spreng., *Dryas octopetala* L., *D. Drummondii* Richards, with occasional plants of *Shepherdia canadensis* (L.) Nutt., representing a pioneer undergrowth stage, alternated with areas of bare talus. A few individuals of *Pyrola uliginosa*, *P. secunda* L., and forest mosses indicated the approaching dominance of the true forest undergrowth.

At the foot of this slope there is a large accumulation of talus in the form of a ridge, parallel to the slope but separated from it by a depression some scores of feet wide. The reason for the separation is quite possibly to be found in the probable former presence of a large snow bank, over the surface of which the fallen blocks rolled. The disappearance of the snow bank with change of climate has left the talus accumulation separated from the main slope by a considerable depression. This explanation has been applied with plausibility to similar cases elsewhere. At any rate, the present accumulation is certainly talus, and it bears climax forest fully developed. Because of its location in the tension belt between the two zones, trees of both are present. *Picea Engelmanni* is most abundant, and *Abies lasiocarpa* is second. *Pseudotsuga mucronata*, *Thuja plicata*, *Pinus Murrayana* Oreg. Com., and *Betula papyrifera* complete the list. *Abies* and *Thuja* are most important in the young growth, and both reproduce abundantly by layering. The shrubs are *Ledum groenlandicum* Oeder, *Menziesia ferruginea*, *Fatsia horrida*, *Viburnum pauciflorum Pylaie*, and *Juniperus sibirica* Burgsd.

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The lower plants include *Linnaea borealis* L., *Pyrola chlorantha*, *Phegopteris Dryopteris*, *Cladonia* spp., and the climax forest mosses, most important among them being *Hypnum cristacastrensis* L. Large talus blocks are everywhere in evidence,

Fig. 2. Climax forest upon talus: *Picea Engelmanni*, *Thuja plicata*. Near Lake Kinney.

but are thoroughly covered with mosses. The soil between the blocks is practically pure humus. This then is apparently the condition toward which the talus areas above are slowly progressing.

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West of the area just described, across the shingle flat, upon the spur that descends from Mt. Whitehorn, is a talus cone of exceptional interest. It is remarkably symmetrical in form, and

Fig. 3. Talus cone northwest of Lake Kinney. Birches at right and near top of cone; climax forest (partly burned) in center. Lake Kinney shingle flat below, bordered at base of cone by subclimax forest.

upon it the birch and conifer stages are very plainly seen. Where the slide is most active, falling material has kept certain paths free of all vegetation. Between these strips grow lines of birches. Over a part of the cone the violence of the rock bom-

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bardment has diminished, because of gradual decrease of slope and resistance offered by the vegetation. Here birches are at the top of the vegetated area, where the brunt of the bombardment must be borne. Below is an area of mature climax forest, which unfortunately has been partly burned. The trail to Robson Pass crosses this cone and affords an excellent opportunity for observation.

Below the cliffs at Emperor Falls, well within the lower limits of the Subalpine Zone, is a fine piece of climax forest developed upon talus. *Picea Engelmanni* is dominant among the mature trees. *Abies lasiocarpa* is less common in mature condition, but in young growth is very abundant. Layered masses of it are so dense as to be penetrated with difficulty. The herbaceous growth is similar in character to that of the area near Lake Kinney. *Fatsia* is absent however.

3. The Moraine Succession

The series of moraines bounding the forefront of the Robson Glacier presents unusual opportunities for study, not the least important being that the usual camp ground is but five minutes walk distant. The Robson Glacier, approximately five miles long, pushes its lower end to the summit of Robson Pass, the altitude of which is 5550 feet (1708 meters). Its front is a little more than half a mile (approximately 1 km.) in extent. The zone of recent moraines that bounds its front is in most places about a quarter of a mile wide, and the recessional ridges are five in number, including that upon which the edge of the ice now rests. At one point near the northeast end of the front there is a projecting knob of rock just beyond the ice edge, and the series of moraines, much compressed, passes over its summit, widening upon each side. The ice did not entirely override this knob in its recent advance. Upon its leeward slope there is a small but exceedingly luxuriant patch of climax forest, in which the ground is deeply covered by mosses. Layered *Abies lasiocarpa* is very abundant here. The contrast between this and the immature climax forest upon the recent moraines is very striking.

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The present series of moraines is very recent and owes its distinctness to a recent minor advance. Just before the present series began to come into being, the ice had retreated to a point within at least the outer boundary of the oldest of the now existent moraines. This is proved by the fact that this moraine has been laid down upon a shingle flat which must have been an outwash plain. Shallow drainage channels cut into this flat

Fig. 4. Moraines and shingle flat of Robson Glacier. Rock knob with patch of climax forest at left. The five moraines may be distinguished: the oldest, with dark forest; the second, very narrow, a dark line of thicket; the third and fourth, apparently without vegetation; the fifth beyond the outlet stream, the ice resting upon it. The dark portion of the shingle flat, protected by the moraines, bears patches of forest and thicket; the light portions have been recently denuded by torrents. At the right, early stages of the Shingle Flat Succession; Berg Lake at extreme right. Photograph by Frank M. Warren.

are seen to disappear beneath the edge of the oldest moraine. No signs of earlier deposits were found, though remnants probably exist at many points along the sides of the cañons. The glacier therefore, not long ago, having retreated to a position somewhere near its present limit, advanced a short distance and deposited a morainic ridge upon the shingle flat. Upon most of the front the ice advanced considerably beyond the rock projection mentioned above, so that its outer limit bulged on each

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side of it. During the retreat from its maximum recent extension to its present position the ice front paused or advanced slightly several times, so that there are now five parallel morainic ridges, very distinct along most of their extent, but close together and confused upon the summit of the rock knob.

To determine the rate of recession of the ice front, measurements were made in 1911 and 1913 by members of the Alpine Club of Canada. These show that at the point where the observations were made the total recession for the two years was 28.4 feet (8.7 meters). A study of tree ages upon the various moraines has furnished some data that throw light upon the average rate of retreat during the period of recession from the oldest recent deposit. The following table gives a summary of the counts. Large trees were cut with an axe 8 to 12 inches above the ground; very small ones were uprooted and counted at the surface. Allowance must be made for this difference, which will add some years to the large trees, and thus make the recessional rate still slower.

Counts of tree ages—all Picea Engelmanni

MORAINE I		MORAINE II		MORAINE III		MORAINE IV		SHINGLE FLAT	
Diam.	Age	Diam.	Age	Diam.	Age	Diam.	Age	Diam.	Age
inches									
13	116	2	30	⅝	82+	⅛	13	15	257
10	108	1½	62	½	26			15	174
7	100	1	41					10	117
6	100								
9	94								
7	84								
6	82								
3	73								
Average	95								183

The small tree on moraine III, which was more than eighty-two years old, is the most important. This was approximately 500 feet from the ice front. It is therefore certain that more—doubtless considerably more than eighty two years have

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elapsed since the deposition of moraine III, and that the average annual rate of retreat since that event has been less than 6.1 feet (1.9 meters)—probably considerably less. If then the Alpine Club record of 14.2 feet (4.35 meters) per year is a true sample of the rate for the whole front, the present rate of recession is very far above the average, in which pauses and perhaps slight advances must be reckoned.

The natural way of approach to the Robson moraines is from the shingle flat. The first and oldest has an abrupt front ten to fifteen feet in height, and is about 300 feet (100 meters) in width. Its surface shows the usual hillocks and kettle holes, and the materials of which it is composed are mostly small and well compacted. Just beyond the first moraine is a silt-filled depression, and next to this the second moraine—a small one, 75 to 100 feet (23 to 30 meters) wide, with an abrupt front ten feet in height. A second depression is followed by the third moraine, the most massive of all, in width equal to the first, and with a front slope 40 to 50 feet (12 to 15 meters) high. The fourth is similar in proportions to the third. The ice rests upon the fifth, which is separated from the preceding by a depression in which flows for half the width of the ice front the main outlet stream of the glacier.

Travelling in reverse direction, from youngest to oldest deposit, we will now trace the development of the Moraine Succession. The fifth moraine, upon which the ice now rests, is very difficult of access because of the outlet stream, and is probably entirely bare of vegetation. The fourth, viewed from even a short distance, would also appear to be without plants. Careful search however over a considerable area—an acre or two—revealed the presence of a few scattered individuals—about one hundred in the space examined. Willow seedlings were present, and also *Epilobium latifolium* L., *Castilleja pallida* Kunth, *Saxifraga aizoides* L., *Lychnis apetala* L., and a single seedling of *Picea Engelmanni*, thirteen years old. It is worth noting that a spruce cone was found upon the iceward edge of the moraine, close to the outlet stream. The plant population upon the fourth moraine is so sparse and so varied that it is impossible

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to define a true plant community. There are potentially three communities, represented by the herbs, the shrubs, and the one or more trees.

Upon the third moraine we find the first definite plant community. Here the vegetation is sparse enough, but is much more abundant than upon the fourth, and certain species emerge as true dominants. These are creeping shrubs and herbs, and I would name the community, from its two most important species, the *Dryas octopetala–Arctostaphylos rubra* Stage of the Moraine Succession. Other members, less abundant, are *Dryas Drummondii*, *Epilobium latifolium*, *Hedysarum Mackenzii* Richards, *Castilleja pallida*, *Silene acaulis* L. It is hardly more than a rudimentary community upon the third moraine, but in development is decidedly in advance of the shrubs and trees, which are represented by occasional willows and very occasional spruce seedlings.

Coming to the second moraine we find a great advance. The difference is so great that the third and second moraines are plainly distinguishable at a distance of two miles by the different amounts of vegetation which they carry. The *Dryas–Arctostaphylos* community is far better developed than upon the third moraine, large areas being dominated by it. But it is now in competition with a second community made up of shrubs; among which several species of *Salix* are the most important. *Betula glandulosa* Michx. is occasional, and increases as the community grows older. These form a true thicket which is the dominant growth upon the second moraine, although comparison with the first moraine shows that it has not yet attained its full development. It may be termed the *Salix–Betula glandulosa* Stage of the Moraine Succession. The trees are also represented here. They are larger and more numerous than upon the third moraine, but are not yet seriously competing with the shrubs. Frequent young spruces were seen, the largest being six feet in height. A few seedlings of *Pinus albicaulis* were also found. Some of the spruces were prostrate and sprawling. Humus is naturally not abundant upon the second moraine, and there are still considerable areas nearly bare of plants.

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The vegetation of the first and oldest moraine merits a detailed description. The whole extent is uniformly covered by what is apparently an open forest in which *Picea Engelmanni* is greatly predominant. *Pinus albicaulis* and *Abies lasiocarpa* are occasional. The trees are small, ranging up to thirty feet (6 meters) in height, and in age to 116 years, as far as investigation went. They stand on the average perhaps thirty feet apart. No old dead trees were seen. There is nearly everywhere between the trees a dense thicket growth made up of

Fig. 5. Moraine II. Thicket of *Salix* and *Betula glandulosa;* a single young spruce. In the background, Moraine III.

several species of *Salix*, *Betula glandulosa*, *Shepherdia canadensis*, and *Juniperus sibirica*. In occasional openings among the trees and shrubs are patches of herbs and creeping shrubs: *Dryas octopetala* and *Arctostaphylas rubra* (Rehder and Wilson) Fernald [*Mairania alpina* of authors], most abundant; *Dryas Drummondii*, *Hedysarum Mackenzii Arctostaphylos Uva-ursi*, *Castilleja pallida*, *Pyrola uliginosa*, *Moneses uniflora*, and a few mosses and cladonias. Humus is fairly abundant in depressions, but scarce in other places. There are frequent small areas,

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especially on hillock summits and on the outer slope, that are entirely bare of plants and humus.

It is at once evident that upon this moraine the two communities already described are still existent. The *Dryas–Arctostaphylos* Community, though well developed in certain spots, has long passed its period of dominance. The *Salix–Betula* Community is far better developed than upon the second moraine. But it in turn is here in serious competition with a third community, the Climax Forest, which is represented by *Picea*, *Pinus*, and

Fig. 6. Vegetation upon Moraine I. Open forest of *Picea Engelmanni* and thicket of *Salix* and *Betula glandulosa*.

Abies, and by *Pyrola* and *Moneses* in the undergrowth. Sufficient time has not elapsed since the deposition of the first moraine to allow the forest to attain to its fullest perfection, but the trend is plainly towards its establishment, with the consequent elimination of the two earlier stages.

The Moraine Succession thus includes three stages: 1. *Dryas–Arctostaphylos;* 2. *Salix–Betula;* 3. Climax Forest. All these have their beginnings together upon the bare moraine, and all are still existent upon the oldest deposit. They attain domi-

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nance in the order given above, because of differences in rapidity of development, the smallest plants first, then the shrubs, and finally the trees. The period of dominance for the first and second stages does not coincide with the period of most perfect development. The *Dryas–Arctostaphylos* Community is the dominant community upon Moraine III because the others are rudimentary. It is a much more solidly developed community in the spots where it occurs upon the older moraines, but upon these it is losing ground in competition with the shrubs and trees. The *Salix–Betula* Community, clearly dominant upon Moraine II, is found in its best development upon the oldest moraine, but is here overtopped and doomed to supersession by the Climax Forest.

4. The Shingle Flat Succession

The shingle flat is one of the most characteristic features of glaciated mountain regions. Morainic material is being constantly carried from its place of deposition by the torrential streams from the glaciers. Much fine silt is borne by the streams themselves as they issue from beneath the ice. All these materials are carried for greater or less distances, and in deposition are roughly sorted through differences in velocity and volume of the flowing water, so that a deposit in a given spot is likely to be rather uniform in size of component materials. Wherever conditions are such that a stream becomes overloaded we find shingle or silt flats. The characteristic grade profile of a glaciated valley with its long stretches of gentle gradient separated by step-like cliffs gives ample opportunity for the deposition of stream-borne materials; so that a river valley below a glacier is likely to be a more or less interrupted flood plain, with numerous meandering and anastomosing streams flowing upon it. The abundance of lakes in glaciated regions, with the consequent slackening of current of the inflowing streams, also favors the formation of alluvial flats. The square-cut upper ends of many alpine lakes are a familiar consequence of this. The present study covered a fine series of shingle flats along the Grand Fork

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of the Fraser, extending from Lake Kinney to its source, the Robson Glacier. The term "Shingle Flat Succession" is used to include the processes upon all the alluvial deposits, whether composed of fine silt or of coarser materials properly termed "shingle."

The normal beginning of the Shingle Flat Succession is upon materials wet by surface or superficial underground flow. The velocity of the surface flow may of course be so great as entirely to prevent the establishment of vegetation. In such a case no invasion can take place until the current slackens.

The pioneers differ according to the size of materials. In true shingle the two most important are annuals: *Epilobium latifolium* and *Saxifraga aizoides*. A species of *Salix* appears almost if not quite as soon as these two. In fine silt the first arrivals are more numerous in species, and are mainly perennials of sedge or rush type. Most important are *Carex pauciflora* Lightf., *Eriophorum* sp., *Equisetum variegatum* Schleich., *Triglochin palustris* L., and *Juncus* spp. The loss of my plant collection is felt here with particular keenness, and in the willow thicket stage as well.

Regardless of size of materials, the next stage upon wet alluvial deposits is a willow thicket, made up of several species. *Betula glandulosa* is added, and the climax forest follows.

Such, in skeleton form, is the Shingle Flat Succession upon wet deposits. Important variations in it are brought about by the continued activity of the streams flowing over the flat. Sooner or later, at some flood time, or merely because of increase of velocity due to partial loss of load, the streams will cut into the alluvial deposits, leaving large stretches of them as low terraces. The moisture conditions immediately change in an important way. The sinking of the streams lowers the water table, and the surface of the terrace becomes relatively xerophytic. The coarser the materials, the more rapidly and thoroughly does this change take place, since capillary rise of water varies inversely with size of materials, and drainage varies directly with it. In such a case the wet flat pioneers are replaced by another set of plants, among which *Dryas Drummondii* is of supreme

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importance. The flat above Lake Kinney is an excellent example. The lower portion, overflowed, or so near the water level as to be very wet, bears the wet-flat pioneers. The main body of the flat, especially the western portion which has long been free from overflow and which is decidedly above the level of the flowing water, is covered by an almost continuous mat of *Dryas Drummondii*, with very little else. This species forms roughly circular patches which continually grow larger. In many places these have grown into contiguity, while in others

Fig. 7. Dry shingle flat at head of Lake Kinney. *Dryas Drummondii* community invaded by *Picea Engelmanni*.

areas of bare shingle separate them. Occasional specimens of *Arctostaphylos Uva-ursi* and *Juniperus sibirica* grow with the *Dryas*. Here the willow thicket stage is eliminated, and its place is taken by a relatively xerophytic forest stage. This subclimax community is characterized by the addition of *Pinus Murrayana* and *Betula papyrifera* to the climax species (here principally *Picea Engelmanni* and *Pseudotsuga mucronata*). All these except *Pseudotsuga* are found as scattered invaders far out in the area dominated by *Dryas*. Along the edge of the

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Kinney flat next to the mountain slope is an older terrace a couple of feet higher than the main body of the flat, and upon this the subclimax forest of *Pinus Murrayana*, *Betula papyrifera*, *Populus balsamifera* L., *Picea Engelmanni*, and *Pseudotsuga* is well developed. *Salix* spp., *Juniperus sibirica*, *Shepherdia canadensis*, *Viburnum pauciflorum*, and *Lonicera involucrata* (Richards) Banks accompany the foregoing, and the ground cover is composed mainly of *Dryas Drummondii* (most abundant, and relict from the earlier stage), *D. octopetala*, *Arctostaphylos Uva-ursi*, *A. rubra* (*Mairania alpina*), *Pyrola uliginosa*, *Orchis rotundifolia* Pursh, *Cornus canadensis* L., *Linnaea borealis*. The line between the subclimax forest and the area dominated by *Dryas Drummondii*, marked by the low escarpment of the older terrace, is quite distinct.

In the westernmost corner of the flat there is a remnant of forest that was formerly true climax except that a few large specimens of *Populus balsamifera* and perhaps other subclimax trees were present.

We thus see that the change from the wet to the dry flat results in a changed succession, *Dryas Drummondii* replacing the wet-flat pioneers, and a xerophytic forest stage taking the place of the willow thicket. It may well be that this course of succession is commoner than the other, since all flats are likely to become dry at some point in their history, and frequently this happens at a very early stage. In the Subalpine Zone the stages upon dry shingle are somewhat different, as will appear in the next paragraph.

The shingle flat which covers the summit of Robson Pass possesses some features of special interest. The general character of the drainage from the Robson Glacier has already been described, and the fact was mentioned that a large area of the flat in front of the terminal moraines has been protected by them from erosion ever since the oldest deposit was made, the evidence for this being found in the shallow stream depressions in the flat which end abruptly against the outer face of the moraine and which manifestly are continued beneath it. Upon this protected area various stages of the Shingle Flat Succession may

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be seen. Beginning with the latest, we find poorly developed areas of climax forest of the subalpine type. *Picea Engelmanni* is by far the most abundant, but *Abies lasiocarpa* and *Pinus albicaulis* also occur sparingly. The trees are widely scattered—much more so than upon the neighboring moraine, and between them is found the same thicket growth that occurs upon the moraine. *Betula glandulosa* is dominant, and *Salix* spp. and *Shepherdia canadensis* are common. The soil to a depth of two or three inches has much humus, and the ground cover is

Fig. 8. Shingle flat protected from erosion by moraines of Robson Glacier. At right, poorly developed climax forest and Salix-Betula thicket; at left, lane-like opening with sparse vegetation—a premorainal stream channel.

fairly continuous. *Dryas octopetala* is commonest, and *Dryas Drummondii*, *Arctostaphylos rubra*, *Hedysarum Mackenzii*, *Silene acaulis*, and *Castilleja pallida* occur frequently. This forest of poorly developed climax nature is found in irregular patches upon the areas a trifle higher than the rest. Between them are anastomosing channel-like slight depressions, which if traced to the moraine are seen to disappear beneath it. These are practically treeless except for scattered young spruces, and the effect is of lane-like openings between patches of large trees and

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thicket. In these lanes the same shrubs occur but they are scattered, not forming thickets. The ground cover is similar but very sparse, there is little humus, and areas of bare ground are frequent. The conclusion is plain that these lanes are deserted shallow stream channels, cut below the general surface, and that the surfaces between them are therefore older. Naturally the succession has progressed to a later stage upon the latter.

The interesting feature is in the comparison of the successions upon shingle flat and moraine. In general character they are much alike, in stages and in species. It has been shown that the moraine habitat is much younger than the shingle flat, since it has been dumped upon the latter, the surface of which has not been appreciably changed since that event. The vegetation however has progressed to a much later stage upon the younger habitat, the moraine. The trees, though somewhat smaller and decidedly younger than those of the flat, are many times more numerous. The thicket growth is much denser, as is also the ground cover. Upon the oldest moraine eight trees ranged in age from 73 to 116 years, with an average of 95 (see table, p. 225) Upon the shingle flat, close to the moraine front, three trees ranged from 117 to 257 years, with an average of 183. Upon the moraine, the rings of five out of six trees examined carefully showed increasing growth rate with increasing age, indicating rapidly improving conditions; while upon the flat the trees examined showed no such change. Further, dead and rotten trunks are common upon the flat, showing that the present generation is not the first, while upon the moraine none were seen. The conclusion is plainly that the succession upon the moraine goes through its development much more rapidly—probably in a small fraction of the time required by the almost identical process upon the shingle flat. At least one plausible reason for this difference is apparent. The shingle flat, being close to the glacier, is composed almost entirely of coarse materials, the fine silt having been carried to much greater distances by the swift streams. The moraine on the other hand is composed of coarse materials, embedded in large quantities of fine silt, upon which swiftly flowing water has not as yet had an opportunity to act.

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Difference in size of soil particles, expressing itself in difference in water retaining capacity, to the advantage of the moraine, seems to be at least a part of the explanation.

The effect upon the succession, of destruction wrought by drainage changes is well shown in parts of this flat which have not enjoyed the protection of the terminal moraine. Both erosion and deposition take place, and both are destructive. In one place a layer of cobbles a foot deep had been deposited upon the old pre-morainal surface, and a torrent had recently cut through the superficial layer and into the older substratum, resulting in total destruction of the vegetation in the area affected by the torrent. In the cut bank exposed by the stream it was shown that partial burial of the woody vegetation does not necessarily destroy it. Willow shrubs were traced to their point of origin in the humus filled upper layer of the pre-morainal deposit. The portions of the stems surrounded by the superficial coarse deposit had produced abundant adventitious roots, and the shrubs were in flourishing condition. Stretches of willow thicket with scattered spruces were seen, the bases buried under coarse shingle, but growing vigorously. In such places the development of ground cover must begin again with the dry shingle pioneers. Owing to a recent drainage change, the main outlet of the glacier is now rapidly destroying a large area of shingle flat forest, leaving in its place an expanse of cobbles. Such a habitat offers the very worst conditions for the establishment of vegetation, and the succession upon it will be an exceedingly slow one.

5. Secondary Successions

Under this heading I am able merely to state that the region offers excellent opportunities for the study of Burn and Avalanche Successions, the latter being specially well shown upon the slopes surrounding Lake Kinney.

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SUMMARY

In the mountains of the Mt. Robson region there are two forest zones. In the lower, or Montane, the dominant and climax formation is made up of *Thuja plicata*, *Picea Engelmanni*, *Tsuga heterophylla*, *Pseudotsuga mucronata*, and *Abies lasiocarpa*. This forest is very similar in character to that of the lower zone of the Selkirks. Its upper limit is approximately 3500 feet (1077 meters). The climax forest of the upper or Subalpine Zone, whose upper limit is 6500 feet (2000 meters), is much poorer in number of species and in size of trees, which are *Picea Engelmanni* (dominant), *Abies lasiocarpa*, and *Pinus albicaulis*. The successions in the two zones are similar in general, but differ in certain details. They are studied to the best advantage in the Subalpine Zone and in the upper parts of the Montane, since the earliest stages, following the retreat of the glaciers, are still present in these regions.

Two primitive surfaces are left bare by the retreat of the ice: rock surfaces and moraines. Each of these soon generates another, so that four habitats are offered to invasion by plants: rock surfaces and talus; moraines and shingle flats. Talus and shingle flat are continually increasing at the expense of rock surface and moraine. In each of these a succession originates, and all of them lead to the establishment of the climax forest.

The successions are all short and much telescoped.

The Rock Surface Succession was not studied.

The course of the Talus Succession upon the lower slopes of Mt. Robson, where the blocks are of medium size, includes no pre-forest stage of consequence. Trees and tall shrubs are the first arrivals: *Betula papyrifera*, *Salix* spp., and the climax conifers. At first *Betula* is greatly predominant because it is not permanently harmed by falling and rolling rock fragments; while conifers are killed thereby. Later, because of lessening bombardment or partial protection by birches or both, the climax conifers attain dominance. Up to this stage the surface of the talus slope may be practically bare of lower growth. The undergrowth follows the trees, and the last plants of the final stage to become established are the climax herbs and mosses.

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The Moraine Succession, as seen upon the five recent moraines of the Robson Glacier, comprises three telescoped stages, having their beginnings at the same time, representatives of all three being present upon the moraine most recently deposited. The stages attain dominance in successive order. The first community to become recognizable is characterized by the ground-shrubs *Dryas octopetala* and *Arctostaphylos rubra*. This is followed by a tall shrub stage including several species of *Salix* and *Betula glandulosa*. The third stage is the climax forest of *Picea*, *Abies*, and *Pinus albicaulis*, which has not yet attained its full development upon these deposits. The spaces between the climax trees are still occupied in part by the *Salix–Betula*, Community, in part by the *Dryas–Arctostaphylos* Community.

The Shingle Flat Succession has its normal beginning upon wet stream-borne deposits. The pioneers differ according to the size of the soil materials. If they are coarse, *Epilobium latifolium* and *Saxifraga aizoides*, both annuals, are the characteristic first arrivals; if fine, perennials of the sedge and rush types are the pioneers. In either case, moisture conditions remaining good, a willow thicket follows these, and is itself followed by the climax forest. If the flat becomes desiccated through down-cutting by the streams flowing over it, a set of relatively xerophytic pioneers replaces the wet shingle species, the most important being *Dryas Drummondii*. In such a case the willow thicket is omitted, and a relatively xerophytic subclimax forest stage is inserted, composed in the Lake Kinney locality of *Pinus Murrayana* and *Betula papyrifera* in addition to the climax conifers. On the dry shingle flat upon Robson Pass the stages are almost identical with those of the succession upon the Robson moraines. The progress of the succession upon the moraine has been much the more rapid, in part at least because the water retaining capacity of the soil is greater, the particles being much finer.

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SOME OBSERVATIONS ON WITCHES BROOMS OF CHERRIES

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The purpose of the present note is to record certain interesting facts that arose in connection with a microchemical study of "witches brooms" of cultivated cherries. It is well known, of course, that these brooms are caused by a certain filamentous fungus, *Exoascus cerasi* (Fcl.) Sad. It was also desired to obtain some additional information in regard to the metabolism of the infected area and to determine, if possible, the cause of the decided red coloration of the leaves of the brooms, especially in their younger stages.

The opinion is still held by some workers that many hypertrophies such as witches brooms do not carry on photosynthetic processes to any appreciable extent. That is to say that the increased growth results practically entirely at the expense of the remainder of the tree. That this is not the case, but on the other hand that there is active assimilation carried on in the broomed portion, has been conclusively demonstrated by Heinricher[1] in a series of simple but interesting experiments.

It is evident to any one who has observed cherry brooms that the leaf buds of the brooms unfold some considerable time before the buds of the normal parts. The almost entire absence of flowers on the broomed area is also plainly evident. The resting winter condition of the broom has been investigated by Schellenberg.[2] By taking portions of the broom and the normal twigs at different times of the winter and placing them in

[1] Heinricher, E., Berichte der Deutschen Botanischen Gesellschaft. Band XXXIII, Heft 5, 1915.

[2] Schellenberg, H. C., Berichte der Deutschen Botanischen Gesellschaft. Band XXXIII, Heft 2, 1915.

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water under warmer conditions Schellenberg demonstrated that the leaf buds of the brooms open some time previous to the normal in the early winter but that this difference in time gradually diminishes towards the normal time of unfolding of the buds.

Smith[3] and others have shown that the storage regions of the brooms have a higher osmotic pressure than the healthy twigs and that they contain a larger amount of storage food than the normal tissue. It is assumed that this increased amount of food accounts for the stimulated growth in diameter.

The latter statement agrees with the observations made by the writer. Twigs from the healthy portion of the tree and from the brooms were gathered April 22 (sunny) at 10 a.m. Sections were made from each and treated with Fehling's solution. On slightly heating, both reduced the solution as indicated by the precipitate found in the cells. This microchemical observation was checked by boiling a few shavings from the respective parts and treating with Fehling's solution in the usual manner. The results confirmed the presence of considerable amounts of sugar in both cases.

In a similar manner cross sections of the normal and diseased twigs were treated with iodine—potassium-iodide. A decided blue black color was found to form in the pith of the sections of the broomed area indicating the presence of considerable amounts of starch. No trace of starch could be found in the twigs of the undiseased parts, even after numerous attempts except in one or two cases were a slight blue coloration indicated the presence of small amounts of starch in the cambium.

The red coloring matter in the leaves also furnishes interesting material for investigation. Even from a considerable distance the red color of the leaves of the brooms is easily discernible. The contrast is especially noticeable when the tree is in flower. The red leaves of the brooms form a conspicuous contrast against the white flowers of the normal twigs.

An alcoholic extract was made from the leaves of the brooms.

[3] Smith, William G., Untersuchen der Mophologie und Anatomie der durch Exoasceen Verursachten Sprosz und Blatt Deformation. Forstlich-naturwiss. Zeitschrift., Bd. III, 1894.

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The leaves chosen had but a trace of green color. The alcoholic extract was a brownish green color. This extract was in turn treated with benzol. The resulting benzol phase was red in color while the alcoholic portion was left a green color. This evidently indicates that chlorophyll is present but is merely masked by the red pigment. This condition is to some extent analogous to that found in the Phaeophyceae and Rhodophyceae, where a brown or red pigment may partially or entirely mask any green coloration that may be present.

The red color is greatly intensified if the benzol phase be slightly acidified. Mineral and organic acids have the same effect. When treated with potassium hydroxide or other alkalies a brownish green color results. The solution on being again acidified becomes a deep red.

These facts naturally lead to the assumption that the red color of the leaves is due to an indicator which is red in acid solution. To demonstrate this point the following simple tests were made. First the benzol phase was tested with litmus. It was acid in reaction. Secondly branches of the brooms which had equally red leaves were placed in water, slightly acid, and slightly basic solutions. The twigs placed in pure water remained unchanged after twenty-four hours. Those standing in the slightly acid solution had the red color in the leaves greatly intensified while those in the slightly basic solution had the red color considerably diminished. If, however, the twigs of the brooms were left standing in water for longer periods of time (one week) the red color gradually disappeared.

Practically the same experiments were tried with the leaves from the normal twigs. These had but a slight red color in rare cases. The benzol phase of the alcoholic extract was light yellow in color although it turned an intensive red on being acidified. The yellow solution was neutral towards litmus.

A very large broom was also found on the native wild cherry (*Prunus emarginata*). A similar red color, although not so evenly distributed through out the leaf, was found in the leaves of the infected area. Alcoholic and benzol extracts showed the presence of the red coloring matter with similar properties to those previously discussed.

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The above observations point towards the following conclusions. (1) They corroborate the assumption that the broom manufactures a considerable amount, if not all of the food necessary for its excessive growth. (2) The increased amount of storage food and the consequent increased osmotic pressure may account for the prolonged and rapid growth of the diseased parts. The influence of an increased osmotic pressure and consequent greater turgidity of the individual cells, if sufficient amounts of water are present—as they no doubt are—may be far reaching. For example it may change the semi-permeability of the protoplasmic membranes and thus decidedly influence the metabolism of the cells. It may also, by tightly pressing the protoplasm against the cell wall and by mechanical stretching, stimulate cell enlargement and division. (3) The fact that the buds on the brooms open before the normal buds indicates that the fungus disturbs the normal periodicity of the affected region. (4) Chlorophyll is present in the leaves of the brooms but is masked by the red color. (5) The red coloration of the leaves is due to the acidity of the leaves, and (6) The red color disappears when the acidity of the leaf is neutralized.

Whether the increase in acidity of the leaves of the brooms is due to the fungus causing certain hydrolytic effects on the stored material, or even the cell walls themselves, is a matter to be cleared up by future investigation. In this connection it is interesting to note that many normal leaves in their young stages have a decided red color, as for example the leaves of the rose, maple, beech, cherry, etc. It may be that the fungus merely prolongs the embryonic condition of the leaves and twigs, since even the leaves of the brooms lose all traces of their red color on becoming fully mature.

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BOOKS AND CURRENT LITERATURE

A FIELD AUXANOMETER.—A short paper has appeared[1] which contains the description of a cheap and, it is claimed, sufficiently accurate instrument for recording growth in the field, when used, of course, with a suitable plant. Indian corn is the one to which the instrument has been adapted. A point of distinct interest is the rigid connection between the writing pen and the growing part. It is estimated that the finished instrument can be had for about $15 a dozen. A cheap clock supplies the motor for the recording drum. While adapted to the purposes of the authors, their auxanometer is not to be thought too generally useful, if the reviewer's experience guides him aright. Every plant presents special difficulties, and when plants and purposes of such a kind are in conjunction, far more delicacy will be required. A one-hour period drum will be found too rapid for some purposes, since the hour-lines may traverse each other, and if growth is slow, an undecipherable record will result. This condition makes amplification also necessary, which is not provided for in the instrument.

The paper includes also a record of one day's growth in Indian corn in the field. Elongation was found to be more rapid in the day than in the night. This, the authors rightly point out, contravenes the generally accepted notion, which, they suspect, has been based on the study of greenhouse plants. It may be indicated however that a good deal of work, by Lock, A. M. Smith, Balls, Blaauw, not to mention some observations of earlier workers, has shown that the aforesaid generally accepted notion is quite erroneous.

Any attempt to adapt or originate instruments which will be useful in the field must be commended both for itself and as an expression of the growing feeling of need for more exact ecological research.—FRANCIS E. LLOYD.

MODES OF RESEARCH IN GENETICS.—It is not often that a conscientious effort is made, in the early stages of the development of a science, to weigh critically the methods of attacking the subject and the philo-

[1] Collins, G. N., and Kempton, J. H., A Field Auxanometer. Jour. Wash. Acad. Sci. 4: 204–209, Apr. 1916.

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sophical interpretation of data. For this reason, as well as because of its intrinsic worth, Dr. Raymond Pearl's Modes of Research in Genetics is especially interesting and valuable.[1] Although problems in heredity have been for ages attractive fields for speculation, the scientific attack upon the general subject of genetics, in a systematic way and from all sides, has just begun. It is particularly fortunate for the science to have near its beginning, a summarization of the modes of research and an estimation of the validity of the deductions, for it will help to curb the careless tendency toward over valuation of certain methods of work and will call attention to the need of careful, logical thought. Such a book as this in almost any other branch of scientific work might have prevented some of the numerous ill advised articles which have so disfigured the history of science and which have precipitated undignified discussions. The fundamental value of this book is very little lessened if one does not agree with the conclusions set forth because it will have stimulated thoughtful consideration of the problems involved. As is natural to expect from the activities of the author, the mathematical point of view is especially emphasized, but other phases of the subject are not neglected.

The first chapter, A Critical Examination of Current Modes of Research in Genetics, defines the problem and summarizes the methodology of the subject. The similarity between members of the same species, the importance of the germ cell, and the development and differentiation of the individual, form the basis of the two conclusions that there are various degrees of specificity of germinal substance, and that reproductive processes tend to maintain this specificity. Biometry, Mendelism, cytology and embryology are each treated clearly to show their essential characteristics and limitations as adapted to genetics. These four are recognized as indirect methods of attacking the question of heredity and a more direct method, through biochemistry is suggested. In the next chapter a detailed discussion of biometry clearly shows how widely this method of study has been misunderstood both by its most ardent admirers and its enemies, and that the need of "quantification" is very great in the biological sciences. Biometry offers primarily a method of describing a group as a group instead of describing it by enumerating the characteristics of the lesser units. It also clearly emphasizes the range of error in any set of observations and gives a means of quantitatively correlating phenomena

[1] Pearl, Raymond, Modes of Research in Genetics. Pp. 182. New York, The Macmillan Company, 1915 ($1.25).

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which are not necessarily related in the chain of cause and effect. The limitations of biometry are shown to be largely those of a descriptive method. The Nature of Statistical Knowledge is next discussed, illustrated by specific examples and with the conclusions that while the description of a group, as accomplished by statistical methods, is a very proper and valuable asset in biological work, on the other hand the prediction of the conditions of the individual, from the data concerning the group, is only an aid to, and not a substitute for, other methods of study of the individual. The problem of inbreeding is discussed in detail particularly emphasizing a "method of measuring the intensity or degree of the inbreeding practiced in any particular case." A "coefficient of relationship" is proposed and illustrated with definite examples, and the consequences of inbreeding, considered as a genetic problem, are discussed. The final chapter of the book shows the practical progress which animal breeding has made independently of genetics, and largely before that science came into existence. However, genetics is of value to the practical breeder in spite of his relatively great progress through empirical methods. Progress in plant breeding has been greatly stimulated, especially by the study of Mendelism, because the plant breeder is unhampered by the restrictions of "pure breed" registering and the attendant difficulties of placing new breeds before the world upon their own merits.

From this short review of the contents of the book it will be seen that while some parts are written particularly for investigators in genetics, parts, at least, are of great interest to the general reader and especially to those engaged in other phases of biological work. The book, as a collection of rather independent essays, is less unified and more unequal in scientific detail than one might desire for a general review of the subject, but it is, nevertheless, a stimulating, critical summary which justified its title.—ERNEST SHAW REYNOLDS.

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NOTES AND COMMENT

At the Quarter Centennial of the University of Chicago, celebrated in June, Professor John M. Coulter was presented with an autograph volume containing records of the careers and work of the 82 men and women who have received doctorates in botany during his headship of the department. At the Conference of the Department of Botany the papers read were: A Quarter-Century of Growth in Plant Physiology, by Professor Burton E. Livingston, of The Johns Hopkins University; The Problems of Plant Pathology, by Professor Frank L. Stevens, of the University of Illinois; and Inland Associations of Algae and their Controls, by Professor E. N. Transeau, of Ohio State University. At the joint Conference of the biological departments the papers read were: Bergson's Philosophy of Instinct as Viewed by an Entomologist, by Professor W. M. Wheeler, of the Bussey Institution; and Genetical Phenomena in Oenothera, by Professor George H. Shull, of Princeton University.

An important feature of agricultural practice in New Zealand consists in the conversion of natural vegetation into areas of permanent pasture, where the topography is too rough to admit of plowing. The small areas of virgin grassland were covered by the coarse bunchgrass *Danthonia raoulii*, which is difficult to eradicate. More extensive areas are covered by the native bracken fern, *Pteridium esculentum*, which gained its dominance through fire or other agencies at a remote or more recent time. The methods employed for the elimination of bracken and the establishment of permanent pasture have been described by Mr. A. H. Cockayne in the June issue of the New Zealand Journal of Agriculture. There are many regions in which the bracken and other ferns are serious weeds, but there are few localities in which an attempt has been made to replace them by instituting a competitive vegetation without the aid of cultivation.

The Ecological Society of America met at San Diego on August 9 to 12, in connection with the annual session of the Pacific Division of the American Association. Two sessions were held for the reading

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of papers, and there were two joint sessions with the Western Society of Naturalists. An afternoon was devoted to an examination of the Scripps Institution for Biological Research, and to demonstrations of the work which is being carried on there. Two days were given to an automobile trip of 200 miles from San Diego across the Cuyamaca Mountains to the edge of the Imperial Valley, returning by a different route. Over thirty local and visiting biologists participated in this trip as guests of the San Diego Society of Natural History, under the leadership of Mr. Frank Stephens.

Efforts are being made to increase the utilization of forest by-products by extracting the oils from pine leaves, as has long been done in the case of spruce and hemlock leaves. These oils are used in proprietary medicines, in perfumes, and in shoe polish. A firm in Oregon has pushed the utilization of yellow pine leaves still further by extracting a useful fiber from the leaf residue after distillation.

In the August issue of The Geographical Review Dr. Stephen S. Visher has contributed a paper on The Biogeography of the Northern Great Plains. The plant and animal life of western South Dakota and the adjacent region has been briefly described, with frequent reference to the controlling physical conditions.

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CONTAINING

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DRY GRASSLAND OF A HIGH MOUNTAIN PARK IN NORTHERN COLORADO

FRANCIS RAMALEY

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The dry grassland here considered is one of a number of associations in a mountain park, Boulder Park, at Tolland, Colorado, the seat of the University of Colorado Mountain Laboratory. In addition to the dry grassland there are sedge moor, willow scrub, meadow and various other[1] plant communities.[2] Since conditions are much the same as in other high mountain parks of Colorado the study bears upon problems larger than those of the immediate locality.

The work on which this paper is based has been carried on regularly beginning with 1912, the most intensive work having been done during the three summers from 1913 to 1915 inclusive. Examination has also been made of dry grassland in other places at altitudes from 5000 feet to 9000 feet, but a report on altitudinal differences is reserved for a later time.

Boulder Park (fig. 1) is an open woodless valley about two miles long and three-quarters of a mile wide closed in by forested hills of pine and spruce. The altitude above sea level at the railway station of Tolland is 8889 feet. This is about 3500 feet above the plains, 20 miles to the east. Through the floor of the park flows South Boulder Creek, here a slow-moving meandering stream, but which in the canyons above and below dashes rapidly along its bed of boulders and broken rock.

At one time local glaciers came down from the Continental

[1] Ramaley, Francis, Remarks on some northern Colorado plant communities, etc. Univ. Colo. Studies 7: 228–236, 1910.

[2] The writer uses the word "community" in a large sense, to mean any definite vegetation grouping; an "association" is a community characterized by broad and general features; while a "society" is a community of rather narrow limits.

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Divide at the west[3] filling the valley with ice and no doubt modifying its topography. Within the park now there are morainic knolls and hollows except where the stream has worked over the deposit leaving low terraces, or where the drying of ancient lakes has exposed their flat beds to be clothed with vegetation. Since none of the hills surrounding the park were glaciated to the top it is to be supposed that their flora was not destroyed during the period of glaciation although probably the climate was cold enough to kill out the more southern types. This is indicated by the present composition of the flora which shows largely northern affinities. When the glaciers finally disappeared there was still at hand a supply of plants to occupy the land exposed.

It will not be necessary here to decide why mountain parks are largely grass-covered rather than forested. The old problem of the prairies is here for solution. That it is by no means a simple problem may be gathered from suggestions that have been offered.[4]

Of the present park grassland some along stream courses or near ponds is mesophytic, being characterized by meadow grasses and sedges and a profusion of flowering herbs forming a close stand with very little bare ground. This may be designated as "meadow." The xerophytic part, which is always rather open, and made up almost entirely of low-growing plants, is in this paper called "dry grassland."

As our discussion proceeds it will be noted that practically

[3] Ramaley, Francis, 1910, l.c.

Henderson, Junius, Extinct glaciers of Colorado. Univ. Colo. Studies **3**: 39–44, 1905.

[4] Shimek, B., The prairies. Bull. Lab. Nat. Hist. Univ. of Iowa **6**: 169–240, 1911.

Gleason, H. A., The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. **9**: 23–174, 1910.

Gleason, H. A., Some unsolved problems of the prairies. Bull. Torr. Bot. Club, **36**: 265–271, 1909.

Pound, Roscoe and Clements, Frederic E., The vegetation regions of the prairie province. Bot. Gaz. 381–94, 1898.

Harshberger, John W., Phytogeographic Survey of North America (Engler's "Die Vegetation der Erde"). Leipsic, 1911.

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all of the plants under consideration are native. European or other "weeds" do not enter into these plant communities; indeed few of them are found anywhere in Boulder Park.[5]

SEASONAL ASPECTS

The growing season in the dry grassland may be considered as consisting of five periods. These, with notes on their most conspicuous and characteristic plants are listed below. The dates given as limits of the seasons are to be considered as merely approximate. In exceptional years there may be a retardation or an acceleration of one or two weeks.

1. Prevernal period (May 1 to June 15). Important plants in flower: *Mertensia bakeri* and *Thlaspi purpurascens*. During the prevernal period the dry grassland is brown with the dead herbiage of the previous year. The bluish-green leaves and bright blue flowers of the low-growing bunches of *Mertensia* are quite conspicuous. Indeed the prevernal might be called the "blue" period. The *Mertensia* is found in old lake beds, along stream terraces and morainic knolls, and in glacial depressions; indeed everywhere in the dry grassland area. The *Thlaspi*, a small, low, white-flowered plant of candytuft-like aspect is more restricted, occurring chiefly on slopes.

2. Vernal period, June 15 to July 1. Important plants in flower: *Cerastium occidentale*, *Antennaria arida*, *Antennaria aprica*, *Carex stenophylla*. This is a period of rapid change in the appearance of the dry grassland. The general brown color of Spring only slightly modified by *Mertensia* and *Thlaspi* becomes replaced by fresh green as the grasses and flowering herbs begin a rapid growth. Chickweed (*Cerastium occidentale*) is scattered nearly everywhere in the dry grassland area, although least abundant in the hyperxerophytic portions on the one hand and in the *Danthonia* society on the other. The species of Antennaria form mats that are conspicuous because of their woolly leaves and white flowers (fig. 3). Since chickweed and the

[5] Elder, Mary Esther, Roadside plants of a high mountain park in Colorado. Torreya, **12**: 175–80, 1912.

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Antennarias are the characteristic plants this is the "white" period in the dry grassland. None of the vegetation reaches to a height of 2 dm., little rises even 1 dm. and most is close-lying. *Carex stenophylla* forms a loose sod. Its small, capitate inflorescences are raised about 5 or 6 cm. above the ground. This plant is frequent in nearly all of the societies of the dry grassland but especially those where conditions are hyper-xerophytic.

3. Early aestival, July 1 to July 15. Important plants in

Fig. 1. General view of Boulder Park looking south-west to the Continental Divide. The dry grassland is situated between the lodgepole pine forest of the surrounding hills and the meadow scrub along the creek. Photo by Prof. G. S. Dodds.

flower: *Aragallus lambertii, Antennaria anaphaloides, A. rosea* and *A. microphylla, Comandra pallida, Sedum stenopetalum, Eriogonum umbellatum.* This is a "red, white and yellow" period. The *Aragallus,* or red loco, covers wide stretches, acres in extent, conspicuous from any vantage point within the park or on the surrounding hills. Where the glacial topography remains the loco is found chiefly on knoll-tops. It occurs especially on east exposures and to the north and south, showing a distinct tendency to be absent from the west slope

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where high winds no doubt cause too great transpiration and too much drying of the soil (fig. 4). In such places there is likely to be much of the *Comandra* and of the species of *Antennaria*, which seem better able to withstand dryness (fig. 2). The flowering scapes of the loco are here about 2 dm. high, while at lower altitudes they are more often 3 dm. Of the species of *Antennaria* only *A. anaphaloides* is of sufficient height to produce

Fig. 2. A patch of the *Muhlenbergia-Antennaria* society on a west-sloping morainic knoll. The light-colored plants with white inflorescences are *Antennaria anaphaloides*.

much effect on the landscape. The *Comandra*, no matter how abundant it may be in places, is not conspicuous, since the dull, greenish-white flowers are small. The brilliant yellow blossoms of *Sedum* form a striking feature of those societies in which this plant occurs in abundance; it is present to some extent nearly everywhere. *Eriogonum umbellatum*, the "sulphur flower,"

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is as a rule confined to the lower slopes of morainic knolls or to sloping banks of the creek, well up from the water but in rather hypoxerophytic conditions. The early aestival period includes the blooming time for a very large number of flowering herbs but none except those already mentioned are sufficiently abundant to make any profound impression on the general aspect of the vegetation.

4. Late aestival period, July 15 to August 1. Important plants in flower: *Festuca* spp., *Poa* spp., *Avena americana, Bromus pumpellianus, Artemisia frigida, A. forwoodii* and *A. aromatica, Campanula petiolata, Orthocarpus luteus.* A general lessening of color occurs during this period. As the grasses become larger the flowering herbs are less conspicuous, besides, fewer of them are now in bloom. The vegetation level is at its height, many of the grasses and other plants rising to 2 dm. above the soil surface. The general average height is, however, much less. Flowering culms of some of the grasses are 3 to 4 dm. tall and the species of *Stipa* sometimes reach even higher. The vegetation cover is more dense than before. But there is still, and always, a considerable proportion[6] of bare ground. This is the "blue and yellow" period, because of the *Campanula* (Fig. 6) and *Orthocarpus.* The two plants are seldom closely associated, although they both occupy hypoxerophytic situations. The yellow of *Sedum stenopetalum* may be continued from the preceding period.

5. Autumnal period, August 1 to October 1. Important plants in bloom; *Muhlenbergia gracilis* and other grasses, *Dasystephana parryi.* The dry grassland shows very little color, the blue gentian, *Dasystephana,* being about the only conspicuous flower. In backward seasons the *Campanula* and *Orthocarpus* of late summer may remain in bloom to about September 1. There is no autumnal flora of yellow-flowered suffruticose

[6] Ramaley, Francis, The amount of bare ground in some mountain grasslands. Bot. Gaz., **57**: 526–28, 1914.

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composites so characteristic of the plains and lower foothills,[7] nor are there grasses that develop autumn coloration of yellow or red as in the meadow and sedge moor of the Park, or even in many dry grasslands elsewhere.

SOCIETIES

Corresponding to the various exposures to wind and sun, to differences in soil texture, soil temperature, and moisture, there are to be recognized certain societies, facies or aspects of the dry grassland. These are not rigidly fixed but show variations and intergradations. Yet in examining any particular part of the dry grassland it is usually possible to determine the society to which it belongs. In the following list for the sake of brevity only a few species are named with each society, although here, as elsewhere in the present study, manuscript notes have been made of all important features. Many of the subsidiary species are almost ubiquitous so far as the communities under consideration are concerned.

1. Erigeron multifidus society. Erigeron multifidus, Potentilla concinna, Selaginella densa, Aragallus lambertii, Carex stenophylla. A type of community that appears on soil recently exposed, as through change in the course of the creek or, in earlier times, a recession of the glacier; frequent on the top of creek bluffs in coarse sandy soil which dries out rapidly. *Aragallus lambertii* and *Selaginella densa* are the commonest plants in this society, but the distinctive species are *Erigeron multifidus* and *Potentilla concinna.*

2. Carex stenophylla society. Carex stenophylla, Artemisia frigida, A. forwoodii and *A. aromatica, Sedum stenopetalum, Chrysopsis villosa, Potentilla hippiana, Potentilla pennsylvanica strigosa, Selaginella densa, Aragallus lambertii.* A community

[7] Ramaley, Francis, Remarks on the distribution of plants in Colorado east of the Divide. Postelsia, **1**: 21–53, 1901.

Ramaley, Francis, Plants of the Florissant region in Colorado. Univ. Colo. Studies **3**: 177–185, 1906.

Vestal, Arthur G., Prairie vegetation of a mountain-front area in Colorado. Bot. Gaz., **58**: 377–40, 1914.

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slightly less xerophytic than the preceding, most often developed on flats or gentle slopes with coarse soil and little humus.

3. *Muhlenbergia-Comandra society. Muhlenbergia gracilis, Comandra pallida, Arenaria fendleri, Antennaria arida, A. aprica* and *A. microphylla, Carex stenophylla, Aragallus lambertii, Koeleria cristata.* Chiefly on slopes exposed to the west wind.

4. *Muhlenbergia-Antennaria society. Muhlenbergia gracilis, Koeleria cristata, Antennaria anaphaloides, Arenaria fendleri, Carex stenophylla, Aragallus lambertii.* Throughout a large part of the season the white inflorescences of *Antennaria anaphaloides* make this grouping of plants conspicuous (fig. 2). Like the preceding society this one occurs chiefly on exposed slopes and knollsides. There is usually a moderate amount of humus in the soil.

5. *Muhlenbergia-Aragallus society. Muhlenbergia gracilis, Aragallus lambertii, Arenaria fendleri, Antennaria* spp., *Carex filifolia, Koeleria cristata, Poa crocata* and *P. rupicola.* The soil is much the same as that of the *Muhlenbergia-Antennaria* society but, as already noted in the account of seasonal aspects, this society develops most often on slopes not exposed to the severest winds.

6. *Muhlenbergia-Danthonia society. Muhlenbergia gracilis, Danthonia parryi, Festuca saximontana, Poa interior, Carex filifolia.* Essentially a grass society with few dicotyledonous plants (fig. 4).

These six societies are listed in order of water requirements. The first is hyperxerophytic, being found only on dry coarse soil and usually in places exposed to rapid evaporation. The sixth develops on soil having some considerable amount of humus. Nos. 2, 3, 4, and 5 are intermediate types; botanists disposed to "lump" might put them all together, or perhaps consider them as subsocieties. No doubt our serial arrangement suggests with a fair degree of accuracy the historical succession of the various societies from their first origin on dry morainal gravel or dry stream terraces. In passing from our No. 1 to No. 6 some may be left out.

Abandoned roads or trails through the dry grassland grow up

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to an earlier type than that through which the road runs, thus in the *Muhlenbergia-Aragallus*, or in the *Muhlenbergia-Danthonia* society an abandoned road most often shows at first the characters of the *Carex stenophylla* or even of the *Erigeron multifidus* society.

So far as can be judged the *Muhlenbergia-Danthonia* society represents the ultimate grassland vegetation of the park. It is found now on older stream terraces and on protected parts of the moraine, in shallow glacial sinks and depressions where washing of adjacent slopes results in an accumulation of humus. It is probable that meadow land also on becoming drained gives rise eventually to a society of this general type, although likely with a greater number of flowering herbs.

Other communities, not a part of the main series noted above, are as follows:

Agropyron association. This community is named as an association rather than a society because of its striking difference in appearance from the societies that have been named, also because of the existence over large areas along the mountain front in the plains region of this "wheat-grass association."[8] Often there is an almost pure growth of *Agropyron smithii* with only a few straggling intruders from the ordinary dry grassland. The *Agropyron* association appears on fine-grained and loose soil, especially where it has been turned up by grading for roads or preparing for foundations of buildings. Probably most of the patches of this association here present have developed since the coming of the white man.

Stipa association. Stipa comata, S. minor, Eriogonum umbellatum, Festuca saximontana. This, like the preceding community, is here named as an association, rather than as one of the societies of the ordinary dry grassland because distinguished by associational rank in the writings of botanists who have studied particularly in the plains region.[9] In some places there are

[8] Vestal, Arthur G., 1914, *l. c.*

[9] Vestal, Arthur G., 1914, *l. c.*

Pound, Roscoe and Clements, Frederic E., Phytogeography of Nebraska, 2nd edition. Lincoln, 1900.

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numerous foothill species in this community, as *Homalobus flexuosus*, *Gilia scariosa*, *Drymocallis glandulosa*. While many plants of the foothills are represented the characteristic short grasses of the foothills are entirely absent, just as they are absent from the entire Park. The *Stipa* association develops only on slopes, especially rolling hills.

Fig. 3. View in the *Carex stenophylla* society showing the abundance of low-growing *Antennaria*. Photograph taken in early June.

Artemisia-Phacelia society. Artemisia frigida, A. forwoodii, A. aromatica, Phacelia heterophylla, Agropyron tenerum. This is an unstable community found on railway fills and in other places where there is freshly-disturbed ground of coarse texture. Perhaps if left undisturbed it would eventually pass to the stage previously named as the *Carex stenophylla* society.

Eriogonum society. Eriogonum umbellatum, Stipa comata and

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S. minor. This is an aspect of dry grassland most often developed on hypoxerophytic slopes and may be considered a more or less temporary community intermediate between the *Stipa* association and the *Muhlenbergia-Danthonia* society of the dry grassland. Whether this ever actually develops into a *Stipa* community seems somewhat doubtful. It is more likely

Fig. 4. *Muhlenbergia-Aragallus* society in the foregound showing flowering scapes of *Aragallus lambertii*. A small patch of the *Muhlenbergia-Danthonia* society is seen farther back where the man is standing. It will be noticed that the plants of the dry grassland are of low growth. The three trees are limber pines, *Pinus flexilis*.

that it passes to the *Muhlenbergia-Danthonia* stage. Plants other than those named are found in the *Eriogonum* society but no one species in considerable abundance. The sulphur flower (*Eriogonum umbellatum*) often forms a horizontal yellow band at the base of a knoll or part way down on a sloping creek-

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bank next to the meadow association. Scattered plants occur also in the various societies of the dry grassland.

Vaccinium society. Vaccinium caespitosum, Androsace puberulenta, Carex siccata. This society develops on east exposures in snow-drift areas where the ground is covered with snow until late in the Spring, and where most of the dry grassland plants are unable to grow because of the short season. The *Vaccinium* is scarcely 5 cm. tall. The standing of this community is somewhat uncertain; it might with propriety be designated as a bit of forest undergrowth from the sub-alpine regions of higher altitudes. It has very little ecological affinity with the ordinary dry grassland.

Vegetation of Fairy Rings. Many fairy rings of the mushroom *Tricholoma praemagnum*[10] are scattered about through the dry grassland (fig. 5). Within the ring there is often a considerable growth of *Artemisia frigida*, and at its margin *Mertensia bakeri, Cerastium occidentale* and *Sedum strenopetalum* are prominent.

ENVIRONMENTAL FACTORS

The climate of Boulder Park is severe. Summers are short, winters are long. There is much wind, especially in winter. Although the precipitation in winter is considerable, much of the snow is blown off from exposed slopes and ridges so that these are bare for weeks at a time during cold weather. The annual rainfall is probably about 28 inches. The largest part of the precipitation comes as snow, much of this during April and May. In summer there are frequent light showers, the moisture from which may not penetrate more than 1 or 2 cm. Mean temperatures for June, July and August are probably about 50°, 57° and 55° respectively and the mean annual temperature about 40°F. All these figures are approximate since exact data are available for temperature only and during the summer months of two seasons. The climate may, however, be judged with a

[10] Ramaley, Francis, Mushroom fairy rings of *Tricholoma praemagnum*. Torreya, In press.

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fair degree of accuracy from comparison[11] with Weather Bureau stations at various altitudes within a radius of thirty miles. Winter is somewhat cooler than winter at Chicago with just as high winds but lower relative humidity; summers are cooler than at Duluth and considerably drier.

All the soil of the dry grassland area is of a sandy nature, with scattered pebbles and even boulders. Little humus is present except is glacial sinks and at the foot of slopes. Determinations of soil temperature and soil moisture have been made during a number of seasons, 1909–15 inclusive. Some of the results have been published.[12] For the sake of brevity only the briefest summary is presented (in table 1).

TABLE 1

Soil temperature in degrees Fahrenheit, 3 dm. below surface

	HIGHEST	AVERAGE	LOWEST
May, 8 readings	66	47	40
June, 15 readings	68	58	49
July, 24 readings	74	64	58
August, 59 readings	69	62	58
September, 13 readings	61	58	55

Water-content studies were made chiefly during June, July and August of 1911 and 1913. The results of 12 determinations for each of five societies is shown in table 2.

TABLE 2

Water content, 3 dm. below surface; in percentages

	HIGHEST	AVERAGE	LOWEST
Erigeron multifidus society	10.8	4.2	0.6
Stipa association	16.0	7.3	2.7
Muhlenbergia-Aragallus society	15.9	7.4	3.3
Vaccinium society	22.0	8.5	4.6
Muhlenbergia-Danthonia society	18.3	8.7	1.8*

* Probably an error. The next lowest was 3.8%.

[11] Annual summaries of the Colorado section of the Climatological Service of the Weather Bureau. U. S. Dept. Agric.

[12] Ramaley, Francis, 1910, *l.c.*

Ramaley, Francis and Mitchell, Louis A., Ecological cross-section of Boulder Park. Univ. Colo. Studies **8**: 277–287, 1911.

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In contrast to these low water contents it may be stated that two of the meadow societies showed averages of 14.8 and 16.7%.

In our previous discussion the *Erigeron multifidus* society was classed as hyperxerophytic. In the main series of succession it was numbered 1, the *Muhlenbergia-Aragallus* society was numbered 5 and the *Muhlenbergia-Danthonia* society 6. It is seen that judgment from appearances as to relative amount of soil water is confirmed by the determinations.

Wilting coefficient determinations[13] of four soil samples were made in the office of Biophysical Investigations, United States Department of Agriculture at Washington through the courtesy of Dr. Lyman J. Briggs. The figures are shown in Table III. It is the greater amount of humus present in the upper part of the soil that raises the wilting coefficient of ordinary dry grassland from 5.1 at 3 dm. to 7.6 at 1 dm.

TABLE 3

Wilting coefficient of soil samples

Erigeron multifidus society, at 2 dm. depth	3.5 ± 0.1
Ordinary dry grassland, at 3 dm. depth	5.1 ± 0.1
Ground-squirrel mound	6.2 ± 0.2
Ordinary dry grassland, at 1 dm. depth	7.6 ± 0.2

Comparison of tables 2 and 3 shows that while usually the water content is ample yet at times it falls below the wilting coefficient. This is most likely to occur in August after the growing period of many of the plants is passed. Occasionally, however, considerable wilting occurs in isolated spots even in July, and long before seeds are ripened.

High winds and low relative humidity are characteristic features of Rocky Mountain climate; evaporation is rapid.[14] To learn the relative amount of evaporation in the *Muhlenbergia-*

[13] Briggs, L. J., and Shantz, H. L., The wilting coefficient for different plants and its indirect determination. Bull. 200, U. S. Dept. Agric., Bur. Plant Ind., 1912.

[14] Ramaley, Francis, and Robbins, W. W., Studies in lake and streamside vegetation, Redrock Lake, near Ward, Colorado. Univ. Colo. Studies **6**: 133–168, 1909.

Ramaley, Francis, and Mitchell, Louis A., 1911 *lc.*

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Aragallus society, which may be taken as an example of average xerophytism and that of the *Muhlenbergia-Danthonia* which is rather hypoxerophytic, determinations were made with porous-cup atmometers. It was found that during the period in which the atmometers were in operation the evaporation in the *Muhlenbergia-Danthonia* association was 69 per cent of that in the other society. The one cup was located on an east-facing slope and therefore slightly protected from west winds while that in the more xerophytic community was on level ground.

Soil moisture and evaporation are often of greater consequence in determining floras than is temperature.[15] But temperature is here very important, for with such cold soil the number of species capable of growing and reproducing is relatively small. It is hoped to extend the study of these various factors in the future.

Some of the plants of the dry grassland would scarcely be abundant save for the activities of ground squirrels, *Callospermophilus lateralis*. These animals are present in great numbers in many parts of the park and form mounds of loose earth where seedlings are easily started. The soil which they bring up from their burrows while coarse-grained does not have the larger pebbles and boulders usually present on the surface. Short-lived plants such as *Polygonum englemannii*, *Chenopodium oblongifolium*, *Gayophytum ramosissimum*, and *Orthocarpus luteus* are likely to find place in this soil. But the plants that most often become established among ground-squirrel diggings are *Artemisia frigida*, *A. forwoodii* and *A. aromatica*. They not only obtain a foothold in new soil as suggested, but if present under the freshly spread ground they may grow up through it while other plants with them are not so able to do this and hence are killed. Any fairly luxuriant growth of these species of *Artemisia* is usually in soil stirred up by ground squirrels. The shrubby cinquefoil, *Dasiphora fruticosa*, when found in dry grassland probably owes its establishment in the area to opportunity for growth of seedlings on squirrel mounds.

[15] Briggs, L. J., and Shantz, H. L., 1912, *l.c.*

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In closing this brief account of the environmental conditions it remains to be emphasized that extreme conditions wherein only highly xerophytic species are found may result from different causes. The texture of the soil is important and in a coarse soil poor in humus extreme xerophytes will be found. But exposure to drying effect of wind is also of consequence and may

Fig. 5. View of dry grassland in which mountain sage, *Artemisia frigida*, is prominent. Part of a fairy ring of mushrooms, *Tricholoma praemagnum*. is seen inclosing the *Artemisia*.

result in such high transpiration that even in fairly fine-grained soil there will be little approach to a mesophytic vegetation cover.

GEOGRAPHIC RELATIONS

Distribution maps (not reproduced in this paper) were made of the 36 most important species of the dry grassland. They

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show the great preponderance of northern plants. Only one of the plants charted (*Muhlenbergia gracilis*) has a distinctly southern extension. Nearly all range considerably farther to the north; 28 extend into Canada, 21 reach in Colorado their southernmost limit. In Table 4 statistics are given of the

Fig. 6. Dry grassland in early August showing *Campanula petiolata* in bloom. The sparseness of the vegetation and its low growth are apparent.

entire 132 species of vascular plants recognized as belonging to the dry grassland. The geographic distribution is taken from Rydberg[16] the altitudinal ranges determined chiefly by personal observation.

[16] Rydberg, P. A., Flora of Colorado, Bull. 100, Colo. Agric. Exp. Sta. Ft. Collins, 1906.

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TABLE 4

Geographic and altitudinal distribution of the dry grassland species

Number of species ranging chiefly to the north	79
Number of species ranging chiefly to the south	7
Number of species ranging to both north and south	46
Number of species ranging chiefly to higher altitudes	10
Number of species ranging chiefly to lower altitudes	43
Number of species ranging about equally up and down	79

FREQUENCY OF OCCURRENCE OF DIFFERENT SPECIES

The plants already mentioned as prominent at the different seasons and those designated as important in the various societies are the ones most noticed in any examination of the dry grassland here considered. Quadrat studies,[17] to determine the relative frequency of different species show that Muhlenbergia is the grass which occupies the greatest amount of ground, while *Carex stenophylla* is of most importance among the sedges. *Koeleria* and the species of *Danthonia*, *Festuca*, and *Poa*, are prominent. Dicotyledonous plants may be mentioned in about the following order: *Artemisia frigida*, *Aragallus* spp., *Antennaria* spp., *Cerastium occidentale*, *Mertensia bakeri*, *Chrysopsis foliosa*, *Sedum stenopetalum*. The relative standing of less important members of the vegetation is difficult to determine and varies much in the different societies or aspects. The only pteridophyte, *Selaginella densa*, is found in nearly every quadrat except such as are in the *Vaccinium* society.

DURATION OF INDIVIDUAL PLANTS

Nearly all the dry grassland plants are perennials; most of them live for many years. Only 12 species, aggregating about 9% of the flora, are annuals or biennials, and even some of these may endure more than two years. They are the following: *Festuca octoflora*, *Hordeum jubatum*, *Polygonum engelmannii*, *Capnoides aurea*, *Arabis connexa*, *Arabis divaricarpa*, *Thlaspi purpurascens*, *Micranthes rhomboidea*, *Gayophytum ramosissimum*,

[17] Ramaley, Francis, The relative importance of different species in a mountain grassland. Bot. Gaz., **60**: 154–57, 1915.

Ramaley, Francis, Quadrat studies in mountain grassland. Bot. Gaz., **62**: 70–74, 1916.

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Androsace puberulenta, Collinsia parviflora, Orthocarpus luteus. Of these short-lived species most are rare or infrequent; only *Orthocarpus luteus* is at all common.

UNDERGROUND PARTS

A study of the underground parts of the 36 most important plants (marked with an asterisk in the systematic list at the close of the article) showed the following features:

	per cent
Shallow-rooted	70
Deep-rooted	30
Stolons present	14
Rhizomes present	33
Rhizomes absent; often a much-branched caudex	53

All the grasses and sedges are shallow rooted and in addition the following: *Eriogonum umbellatum, Cerastium occidentale, Sedum stenopetalum, Mertensia bakeri, Orthocarpus luteus, Campanula petiolata, Achillaea lanulosa, Antennaria* (4 spp.), *Artemisia frigida.* The sedges and about one-half of the grasses spread by rhizomes; the other perennials by innovations at the stem base. Of the dicotyledons in the list only the following have true rhizomes: *Comandra pallida, Cerastium occidentale, Campanula petiolata, Achillaea lanulosa, Antennaria anaphaloides.*

Hyperxerophytic areas have, perhaps, the greater number of deep-rooted plants, as *Potentilla concinna, P. hippiana, P. pennsylvania strigosa, Erigeron multifidus, Chrysopsis villosa.* But in these same situations the shallow-rooted *Selaginella densa* and *Carex stenophylla* occupy much of the ground. Both types of plants have their advantages. Shallow-rooted forms make use of the moisture from light showers which are frequent in the growing season, while deep-rooted plants are able to draw upon the soil water of lower levels.

LIST OF VASCULAR PLANTS OF THE DRY GRASSLAND

The following list includes all vascular plants recognized within the dry grassland of Boulder Park with the exception of a few species occasional along roads or elsewhere and evidently

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not properly a part of the communities under discussion. The nomenclature followed is that of Rydberg's *Flora of Colorado.*[18] Many of the plants have been determined by Professor Aven Nelson of the University of Wyoming and some, especially among the grasses, by Professor A. S. Hitchcock and Dr. P. A. Rydberg. The present writer, however, assumes full responsibility for the accuracy of the determinations, and any mistakes are his, not those of the gentlemen named.

In the list the commonest species are marked with an asterisk (*); names of rare plants, or species seldom found in ordinary dry grassland however abundant elsewhere, are enclosed in parentheses. Figures have the following significance as to flowering period: 1 = Prevernal, 2 = Vernal, 3 = Early Aestival, 4 = Later Aestival, 5 = Autumnal.

**Selaginella densa*, 1
(*Agropyron pseudorepens*), 4
(*Agropyron richardsonii*), 4
(*Agropyron smithii*), 4
Agropyron tenerum, 4
**Agropyron violaceum*, 4
(*Agrostis hiemalis*), 4
**Avena americana*, 3
(*Blepharineuron tricholepis*), 4
Bromus pumpellianus, 4
(*Calamagrostis hyperborea*), 4
(*Calamagrostis purpurascens*), 4
(*Danthonia intermedia*), 4
**Danthonia parryi*, 4
(*Deschampsia caespitosa*), 3, 4
Festuca ingrata, 3
Festuca octoflora, 5
Festuca rubra, 4
**Festuca saximontana*, 3, 4
Festuca thurberi, 3
Hordeum jubatum, 4
**Koeleria cristata*, 4
**Muhlenbergia gracilis*, 4
Muhlenbergia subalpina, 4
(*Poa arctica*), 3
(*Poa compressa*), 4
**Poa crocata*, 3
(*Poa epilis*), 3
**Poa interior*, 3
Poa longipedunculata, 4
Poa pattersonii, 4
**Poa rupicola*, 4
Poa subpurpurea, 4
Sitaniqn brevifolium, 4
**Stipa comata*, 4, 5
Stipa minor, 3
Stipa nelsonii, 3
Trisetum subspicatum, 3, 4
Carex deflexa farwelii 2, 3
**Carex filifolia*, 3, 4
(*Carex marcida*), 4
(*Carex obtusata*), 3
Carex pennsylvanica, 2, 3
(*Carex pratensis*) 4
(*Carex siccata*), 4
**Carex stenophylla*, 2, 3
**Juncus balticus montanus*, 3, 4
(*Juncus confusus*), 3, 4
(*Juncus longistylis*), 3, 4
(*Allium geyeri*), 3
**Allium recurvatum*, 4
(*Calochortus gunnisonii*), 4
**Comandra pallida*, 3
(*Eriogonum subalpinum*), 3, 4

[18] Rydberg, P. A., 1906, *l.c.*

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**Eriogonum umbellatum*, 3, 4
Polygonum engelmannii, 3
Chenopodium oblongifolium, 4
(*Alsinopsis obtusiloba*), 2
Arenaria fendleri, 4
**Cerastium occidentale*, 2
Silene hallii, 4
(*Anemone globosa*), 2
(*Delphinium nelsonii*), 2
(*Pulsatilla hirsutissima*), 1, 2
(*Ranunculus cardiophyllus*), 2
(*Capnoides aureum*), 2, 3
(*Arabis connexa*), 2
Arabis divaricarpa, 2
Erysimum wheeleri, 2
Thlaspi purpurascens, 1
**Sedum stenopetalum*, 3
Micranthes rhomboidea, 2
Dasiphora fruticosa, 3
**Potentilla concinna*, 2
**Potentilla hippiana*, 3
(*Potentilla monspeliensis*), 3
Potentilla nuttallii, 3
**Potentilla pennsylvanica strigosa*, 3
Potentilla pulcherrima, 3
(*Sieversia ciliata*), 2
(*Aragallus albiflorus*), 3
**Aragallus lambertii*, 3
**Aragallus richardsonii*, 3
(*Astragalus sulphurescens*), 4
Homalobus flexuosus, 3
(*Homalobus tenellus*), 4
(*Tium alpinum*), 3
Xylophacos parryi, 3
Gayophytum ramosissimum, 4
Pseudocymopterus tenuifolius, 3, 4
(*Arctostaphylos uva-ursi*), 2
Vaccinium caespitosum, 3
Androsace puberulenta, 3
Amarella plebeja, 5
Dasystephana parryi, 5
(*Gilia scariosa*), 3
(*Phacelia heterophylla*), 3
**Mertensia bakeri*, 1
Mertensia lateriflora, 2
(*Collinsia parviflora*), 2
**Orthocarpus luteus*, 4
(*Pentstemon oreophilus*), 3
Pentstemon procerus, 3
Galium boreale, 3
**Campanula petiolata*, 4
**Achillaea lanulosa*, 4
**Antennaria anaphaloides*, 3
**Antennaria aprica*, 2, 3
**Antennaria arida*, 2, 2
(*Antennaria corymbosa*), 3
**Antennaria microphylla*, 3
(*Antennaria oxyphylla*), 3
Antennaria rosea, 3
Artemisia aromatica, 4
**Artemisia forwoodii*, 4
**Artemisia frigida*, 4
Artemisia gnaphaloides, 4
**Chrysopsis foliosa*, 4
(*Chrysothamnus elegans*), 4
(*Chrysothamnus parryi*), 4
Erigeron flagellaris, 3
Erigeron eximius, 4
Erigeron macranthus, 4
Erigeron multifidus, 2, 3
(*Erigeron speciosus*), 4
Gaillardia aristata, 4
(*Senecio werneriaefolius*), 3
Senecio perplexus, 2, 3
Solidago concinna, 4
Solidago oreophila, 4, 5
Agoseris glauca, 4

SUMMARY

The foregoing pages report an intensive study through four seasons of the dry grassland of a mountain park in northern Colorado at an altitude of about 9000 feet. The vegetation is described as low-growing, consisting largely of grasses and sedges with many profusely-flowering perennials. Five seasonal

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periods are recognized: (1) *Prevernal*, May 1 to June 15, characterized by the blooming of *Mertensia bakeri* and *Thlaspi purpurascens;* (2) *Vernal*, June 15 to July 1, with *Cerastium occidentale*, *Carex stenophylla* and various species of *Antennaria* in bloom; (3) *Early Aestival*, July 1 to July 15, during which there is a profusion of flowers, particularly *Aragallus lambertii*, *Antennaria anaphaloides*, *A. rosea*, *A. microphylla*, *Comandra pallida*, *Sedum stenopetalum*, *Eriogonum umbellatum*, etc.; (4) *Later Aestival*, July 15 to August 1, showing blossoming of many grasses, *Festuca*, *Poa*, *Koeleria*, *Bromus*, *Agropyron*, also the species of *Artemisia* and *Campanula petiolata* and *Orthocarpus luteus;* (5) *Autumnal*, August 1 to October 1, during which time there occurs the blooming and fruiting of *Muhlenbergia gracilis*, the most abundant grass of the park, together with the flowering of a blue gentian, *Dasystephana parryi*. A series of six societies or aspects is noted, corresponding to historical stages from bare soil to the ultimate grassland of the park; other societies, not in the main line of succession, are also characterized. A brief section on environmental factors discusses climate, soil, evaporation, importance of ground squirrels, etc. Accounts are presented of geographical relations, duration of individuals and underground parts of plants. The paper closes with a list of 133 species belonging to the dry grassland, a special designation being made of the 36 most important.

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A STUDY OF THE DEVELOPMENT OF DUMONTIA FILIFORMIS[1]

I. The Development of the Tetraspores

GRACE A. DUNN

The Johns Hopkins University, Baltimore, Maryland

The tetrasporic and sexual plants of *Dumontia filiformis* were found at South Harpswell, Maine, growing in the tide pools and on the rocks exposed to the surf. This paper presents the results of a study of the development of the asexual plants. The discussion of the occurrence of the plant and of other phases of its development will appear later in the Botanical Gazette. The tetrasporic plants usually branch freely (fig. 1, *A*), but mature, simple individuals occur occasionally.

A. THE DISTRIBUTION OF THE TETRASPORANGIA IN THE THALLUS

The tetraspores are embedded in the wall of the thallus. They can be seen without a lens in plants which do not contain too much phycoerythrin, if they are examined in strong light. The tetraspores are distributed evenly all around the wall of the thallus throughout practically the entire length of the branches and the main axis (fig. 1, *B*). In all plants, the more mature tetraspores are found in the upper portion of the branch or main axis and the younger ones toward the base.

B. THE ORIGIN AND STRUCTURE OF THE MOTHER CELL OF THE TETRASPORANGIUM

The mother cell of the tetrasporangium is endogenous in origin. Each cell of a primary subcortical branch often produces a mother cell of a tetrasporangium (fig. 1, *C*). The cells of secondary subcortical branches may also occasionally

[1] Botanical Contribution from the Johns Hopkins University, No. 50.

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give rise to a mother cell. This results in the formation of an enormous number of tetrasporangia. The average number of tetrasporangia in a piece of the thallus 1 cm. long is 25,000.

At an early age the subcortical cell destined to develop a mother cell of a tetrasporangium, can be distinguished from the adjoining vegetative cells of the same rank by its greater size and a difference in staining properties (fig. 1, *C*). The chromatophore of the mother cell of the tetrasporangium is a clathrate, hollow ellipsoid (fig. 1, *C*, *D*). As the mother cell matures, the portions of this ellipsoid become elongated into irregular, narrow bands (fig. 1, *E*). A few linin fibrillae radiate out from the nucleolus to the nuclear membrane. All the chromatin is in the nucleolus, which is never homogeneous and sometimes contains as many as three vacuoles (fig. 1, *F*, *G*). The mother cell of the tetrasporangium up to a fairly late stage in its development remains connected to the cortical cells at its outer end (fig. 1, *D*). None of the mature tetrasporangia show these connections.

C. THE MATURE ONE-CELLED TETRASPORANGIUM

The cell contents. The mature tetrasporangium is 66μ in length and 44μ in width. It is highly vacuolated. The chromatophore and most of the cytoplasm are peripheral. The ribbon-like strips of the chromatophore have, at regular intervals, gradually narrowed and become thread-like. The chromatophore then appears to consist of small irregular plates about 1.4μ in diameter which are arranged in rows and are connected by narrow cytoplasmic threads (fig. 1, *H*). The diameter of the nucleus is 8.4μ and that of the nucleolus is 3.1μ. The number of linin fibrillae is greater than that in the nucleus of the mother cell of the tetrasporangium (fig. 1, *F*, *I*). All the chromatin is in the nucleolus.

The distribution of the chromatin in the tetrasporangium nucleus of *Dumontia* differs, as far as known, from that of all other Florideae. In the tetrasporangium nucleus of *Griffithsia*,[2]

[2] Lewis, I. F. The Life History of *Griffithsia Bornetiana*. Annals of Botany **23**: 639–690. 1909.

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the chromatin is in the form of several spherical bodies which have been formed by a fragmentation of the nucleolus. In *Corallina*,[3] *Polysiphonia*,[4] *Delesseria*[5] and *Nitophyllum*,[6] the chromatin is not contained in the nucleolus, but is present in fine granules distributed along the strands of the linin net of the nucleus.

The nucleus of the tetrasporangium of *Dumontia* is surrounded by a jacket of dense cytoplasm. Shortly before division a number of granules appear at the poles of this jacket and in the cytoplasm at the periphery of the cell. These granules are hollow, 1.4μ in diameter, and stain sharply with haematoxylin or safranin. They are more numerous where the cytoplasm is more dense and consequently are especially abundant at the poles of the cytoplasmic jacket enveloping the nucleus (fig. 1, *J*).

These granules were tested for fat with Sudan III and cyanin, for starch with chlorozinciodide and potassium iodide, for protein with Millon's reagent. The starch and fat tests were negative and the protein test seemed clearly positive, but as the amount of substance stained was so small and the light in which it was observed so intense, the red color was very faint. These bodies are evidently a protein substance. After having been treated with Millon's reagent, the granules and nucleolus in the tetrasporangium of *Dumontia* have the same color. As far as the staining reactions of these granules indicate, since Millon's reagent, haematoxylin, and safranin are nuclein stains, there seems no reason to doubt that they are a nuclein-like substance. However, the volume, the position, and time of appearance of these granules is quite convincing evidence that they are not chromatin material. The total volume of all the

[3] Davis, B. M. Kerntheilung in Tetrasporen. Mutterzelle bei *Corallina officinalis*. Ber. d.d. bot. Ges. **16**: 266–271. 1898.

[4] Yamanouchi, S. The Life History of *Polysiphonia violacea*. Bot. Gaz. **17**: 401–449. 1906.

[5] Svedelius, Nils. Über den Generationswechsel bei *Delesseria sanguinea*. Svensk Botanisk Tidskrift., Bd. 5, H. **3**: 260–324. 1911.

[6] Svedelius, Nils, Über die Tetradenteilung in den vielkernigen Tetrosporangiumanlagen bei *Nitophyllum punctatum*. Ber. d. d. bot. Ges. **32**: 452–456. 1914.

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granules in a cell is about twice that of the nucleolus. They appear in the tetrasporangium before any nuclear division has occurred, and at the time of their appearance the amount of chromatin in the nucleolus does not seem to have been diminished. Bodies which are evidently similar to these granules found in *Dumontia* have been seen by Lewis in *Griffithsia* and by Svedelius in *Delesseria*. They appear in the tetrasporangium in *Griffithsia* at the time of synapsis and disappear at the end of the first reduction division. These granules are at first small and quite numerous, but later they become larger and the number present in the tetrasporangium increases. Lewis believes that they have been derived from the nucleus.

The granules appear in the tetrasporangium in *Delesseria* at the time of diakinesis. As in *Dumontia*, they are especially numerous in the cytoplasmic jacket around the nucleus; and, as Svedelius states, might readily be considered as part of the chromatin contents of the nucleus. These granules, as in *Griffithsia*, are at first small and numerous. Later, there is a marked increase in their size and a decrease in their number. Svedelius is inclined to believe that these bodies did not originate in the nucleus. He thinks their function must be of a nutritive nature, possibly similar to that of the degenerating nuclei in *Martensia*.[7] In *Martensia* there is a marked increase in the volume of the chromatophores and all the cytoplasmic contents of the tetrasporangium during the degeneration of 49 of its nuclei. Svedelius believes that the substance of these degenerating nuclei is used in the formation of this extra amount of cytoplasm.

Evidence concerning the time of nuclear division in the tetrasporangium. Only a few stages of nuclear division in the tetrasporangia have been seen.

Material was collected at each of the twenty-four hours of the day. Five or six whole plants were fixed in each collection. This material was examined and in every case the nuclei in the tetrasporangia and all the vegetative nuclei observed were in

[7] Svedelius, Nils. Über den Bau und Die Entwicktelung der Florideengattung *Martensia*. Kongl. Svenska Vet. Akad. Handl., Bd. 43, no. 7: 1–101. 1908.

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the resting state. It was then thought that the failure to find mitosis might be due to the fact that the collections were not made in twenty-four consecutive hours and that the plants were not taken from the same group in a tide pool or even from the same tide pool. Thus, if mitosis regularly occurs at a certain hour of the night, a change in the intensity of the light of the proceeding day or a change in temperature may so alter the physiological conditions in the plant that the nucleus will divide one or two hours earlier or later than the usual time. The collections in this first series were made on seven different days and it is quite possible that the hour at which mitosis occurred varied somewhat during this time.

A second series of collections was then made. This collection was made during the greatest of a series of spring tides. Five or six plants were fixed at each hour in Flemming's medium chrom-acetic-osmic mixture. It took about fifteen minutes to cut the plants, hence the time elapsing between the successive fixations was about forty-five minutes. The plants were gathered from certain groups in three different tide pools. In six collections which were made at high tide, it was impossible to reach these pools; so the stones on which some of the plants in these groups were growing were for this length of time placed in an artificial tide pool near the shore. The plants cannot be considered as having been placed in abnormal conditions, because even in this artificial tide pool they were covered by as much water and as much exposed to the surf as they were for at least half of the month, in the tide pools in which they grew.

As will be shown later, even from this material very few data were obtained concerning mitosis. Hundreds of tetrasporangia were examined in the material of each of these twenty-four collections. It is very evident that the mitosis occurring in the tetrasporangium nucleus of *Dumontia* must be of exceedingly short duration. In the material collected at 9:00 a.m., a few stages of nuclear division were found. Several tetrasporangia which were one-celled but binucleate were also seen. Since nuclear division in the tetrasporic plants is always immediately followed by cell division, the occurrence of the unicellular,

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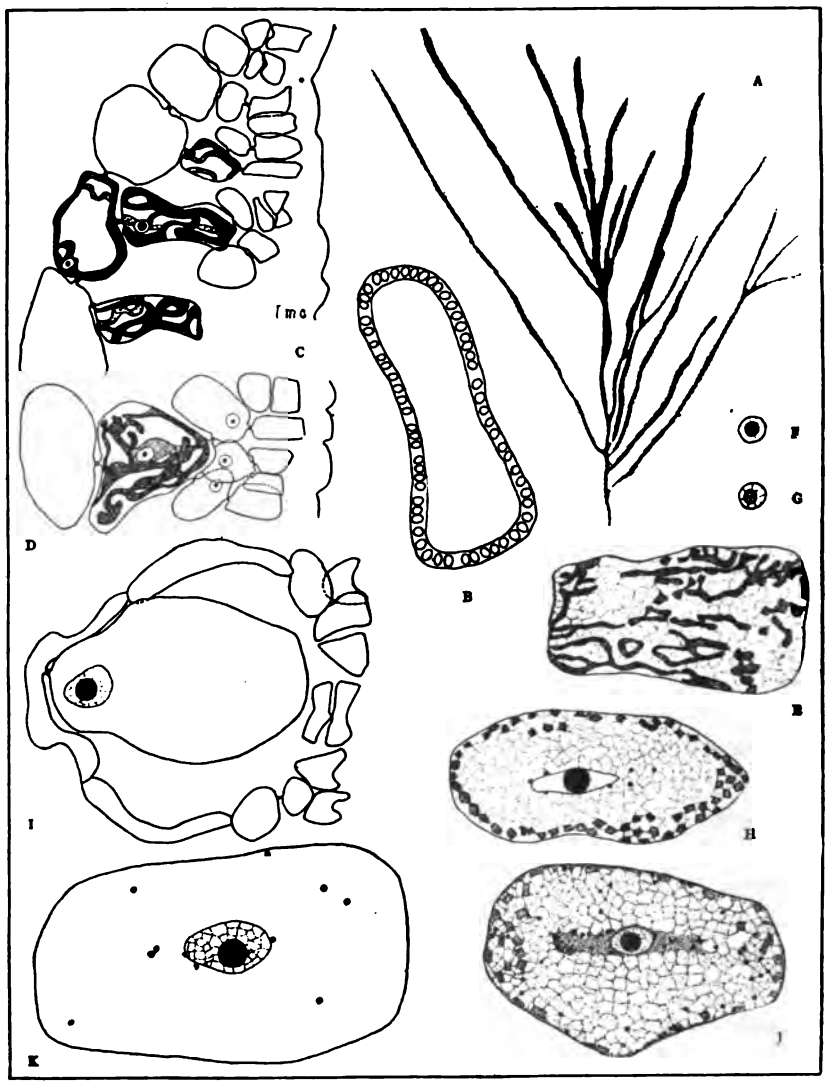

Fig. 1. *A*. Mature tetrasporic plant, showing type of branching and frayed ends of branches. × 0.35. *B*. Diagram. Transverse section through thallus showing distribution of tetraspores. × 250. *C*. Longitudinal section through wall of thallus, showing origin and contents of mother cells of tetrasporangia, t. m. c. × 700. *D*. Longitudinal section through mother cell of tetrasporangium showing connections to the cortical cells at its outer end. × 1000. *E*. Surface view of tetrasporangium, showing cytoplasmic net, position and structure of

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binucleate tetrasporangia would indicate that mitosis had just taken place.

Other workers on the Florideae have experienced some difficulty in obtaining stages of mitosis. Lewis reported that practically no mitotic figures were found in material which was kept in running water in the laboratory and fixed at every hour. He did, however, succeed in finding the desired stages in material which he fixed in the field. If Lewis' figures show all the important stages in mitosis as it occurs in the tetrasporangium nucleus in *Griffithsia*, the process is not exactly similar to the reduction division which occurs in most plants. No spireme was seen in any nuclear divisions in *Griffithsia*. Svedelius carefully worked out mitosis in the tetrasporangium of *Delesseria* and failed to find a spireme. He found later in studying tetraspore formation in *Nitophyllum* that the spireme in this form is very delicate and of short duration. Svedelius believes that he may have overlooked the spireme in *Delesseria*. It is conceivable that mitosis in the Florideae is quite similar to that in the higher plants; but in many of the forms it has not been possible thus far with our present technique to detect all the stages, some of which may be of short duration.

The nuclear and cell division. The nucleus in the tetrasporangium is spherical when it first assumes a central position in the cell. The nucleus elongates in preparation for division (fig. 1, *K*). All the chromatin is still in the nucleolus at this stage and the linin network is also present. In the next later stage, the nucleus has assumed a spindle shape. No network is now present and no spindle fibres can be definitely made out, although there is a slight suggestion of the latter. It is difficult to determine the structure of the chromatin mass because it stains

chromatophores. × 700. *F, G.* Nuclei of mother cells of tetrasporangia, showing vacuoles in nucleoli, and linin fibrillae. × 1000. *H.* Longitudinal section through tetrasporangium, showing position and structure of chromatophores. × 700. *I.* Longitudinal section through tetrasporangium, showing jacket of sterile cells, and structure of nucleus. × 700. *J.* Longitudinal section of tetrasporangium showing cytoplasmic net, peripheral chromatophores, cytoplasmic jacket enveloping the nucleus and protein granules. × 700. *K.* Nucleus elongating in preparation for division. × 1000.

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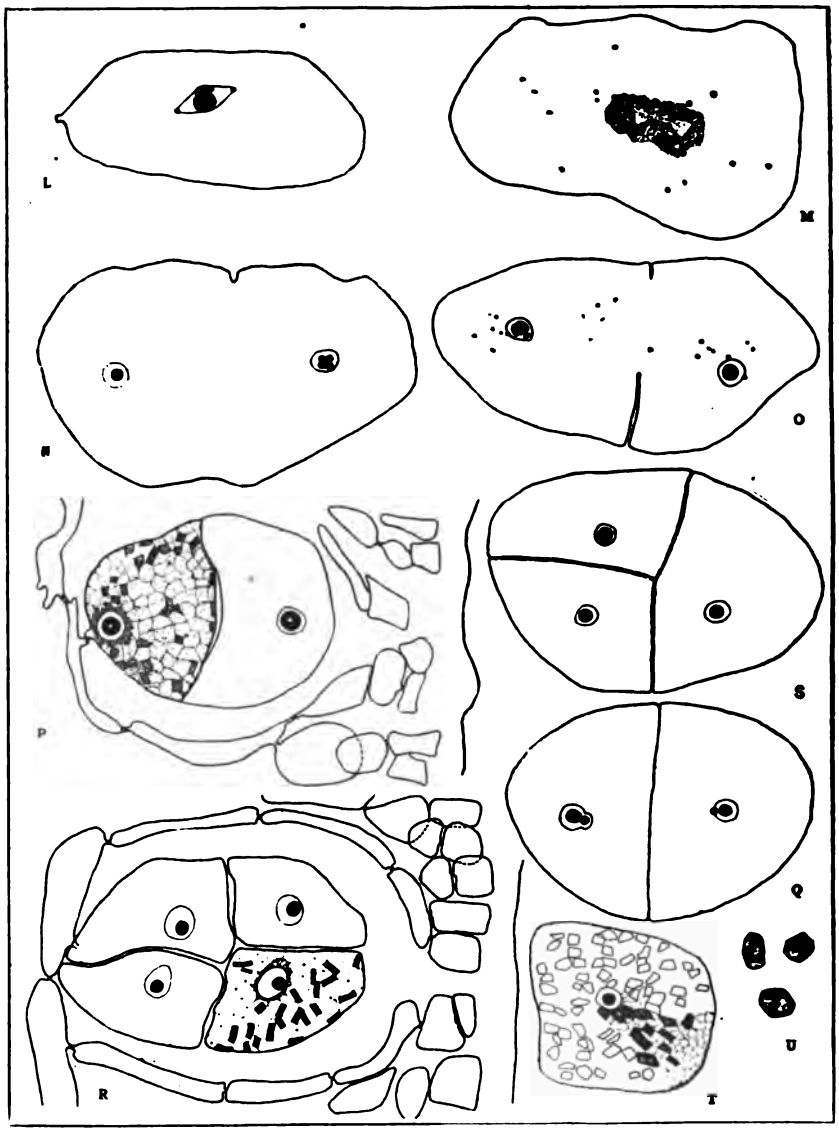

Fig. 2, *L*. Metaphase, centrosomes are present. × 700. *M*. Telophase. × 1000. *N*. Unicellular, binucleate tetrasporangium. × 1000. *O*. First cleavage furrow just being formed in tetrasporangium. Protein granules are present. × 1000. *P*. Longitudinal section of a two-celled tetrasporangium, showing attachment to subcortical cell and a portion of the jacket of sterile cells. Chro-

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very heavily. In a few cases the chromatin appears to be in the form of two spherical bodies of almost the same size (fig. 2, *M*). A small dark staining body is always present at each pole of this spindle-shaped nucleus. These bodies are evidently similar to the centrosomes occurring in the tetrasporangia of *Polysiphonia* (Yamanouchi) and to the few centrosomes seen in *Delesseria* (Svedelius). In both these forms, the centrosomes apparently arise *de novo* and no radiations have been seen running out from one of these bodies into the cytoplasm. Division has occurred in the next stage which was observed and the daughter nuclei are just separating (fig. 2, *M*). The chromatin in each of these nuclei appears to be in the form of a disc which is composed of four granules. No nuclear membrane is present around either of these chromatin masses. The chromatin is on structures which resemble spindle fibres. The cytoplasmic jacket which surrounded the mother nucleus has not begun to divide. Each of the two daughter nuclei moves to an end of the cell before it begins to divide (fig. 2, *N*). The chromatin in the nuclei at this stage may be in one, two or four small round bodies. The diameter of these nuclei is 4.4μ.

At a little later stage the cleavage furrow which will divide the tetrasporangium into two cells is just being formed (fig. 2, *O*). The first cleavage furrow as seen in a cross-section of the thallus is perpendicular to the longitudinal axis of the tetrasporangium, that is, parallel to the surface of the thallus. The cytoplasm of this stage is considerably vacuolated and for the most part peripheral. The chromatophores have apparently decreased in number and they do not stain as readily as they did in the

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matophores are distributed on cytoplasmic net and a number of small chromatin granules are present. × 700. *Q*. Longitudinal section of a two-celled tetrasporangium, nuclei preparing for division. × 700. *R*. Similar section of a four-celled tetrasporangium, showing the jacket of sterile hyphae and the contents of a young tetraspore. × 700. *S*. Similar section of a four-celled tetrasporangium; the quadrant walls are perpendicular to each other. × 700. *T*. Longitudinal section of a mature tetraspore, showing the arrangement of the chromatophores. × 700. *U*. Surface view of chromatophores of a mature tetraspore, showing perforations in their walls.

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younger tetrasporangia. The protein granules are still present, although they have decreased somewhat in size (fig. 2, *O*).

The mode of division in the cases of tetraspore development that have been recently worked out is tripartite. In such divisions, the separation of the tetraspores is not completed until they are discharged. The two cells formed at this first division of the tetrasporangium of *Dumontia* are completely separated.

D. THE TWO-CELLED TETRASPORANGIUM

Cell contents. The cytoplasmic contents of the cells have increased. Chromatophores which stain very faintly are distributed in the cytoplasm lining of the cells and in the strands radiating out from the nucleus. These chromatophores are quite numerous; about 32 occur in a cell. They are considerably flattened and appear as rows of small plates (fig. 2, *P*). The protein granules are still present. They have decreased greatly in size but not in number (fig. 2, *P*). It is quite possible that the function of the protein granules may be similar to that of the granules of *Delesseria*. While these protein granules in *Dumontia* have been decreasing in size, there has been a marked increase in the volume of cytoplasm and the number of chromatophores in the cells. The nucleolus generally contains a vacuole (fig. 2, *P*). A small chromatin granule near the periphery of the nucleus is sometimes present in these nuclei as well as in those of the tetraspores.

Nuclear division. Only one stage in the second nuclear division was observed. In this case the chromatin in each of the two nuclei was in two spherical bodies (fig. 2, *Q*).

The two cells of the tetrasporangium may divide in parallel planes or in planes which are perpendicular to each other (fig. 2, *R*, *S*). The cells are completely separated in these two latter divisions.

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E. TETRASPORES

The cell contents. The cell contents and structure of the nuclei in the tetraspores which have just been formed is quite similar to those in the two-celled tetrasporangium (fig. 2, *P*, *R*). In the mature tetraspore, the volume of cytoplasm and the size of the chromatophores have increased. The protein granules have entirely disappeared. The chromatophores lie in rows, some at the periphery and some in strands of cytoplasm radiating out from the nucleus (fig. 2, *T*). The chromatophores average 3.5μ in length and 1.4μ in width. They are hollow, oval bodies; and round perforations can be seen in the walls of some of them (fig. 2, *U*). Thus they are quite similar to the chromatophores occurring in the vegetative cells, but are very much smaller. The mature tetraspores do not round off while embedded in the thallus.

The discharge of the tetraspores. The tetraspores escape through a pore formed in the outer wall of the thallus. No spores were observed in the actual process of escaping, but many empty tetrasporangia were seen in the cross sections in which mature tetraspores were also present. The ends of the branches are often frayed out (fig. 1, *A*), and it is evident that the tetraspores might thus be torn free along with the vegetative cells of the thallus.

SUMMARY

The mother cells of the tetrasporangia are subcortical cells. The chromatophore of the mother cell segments into a number of parts which persist through all stages of the tetrasporangium and are present in the tetraspores. Mitosis in the tetrasporangium is either not similar to that in the higher plants or is of very short duration.

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BOOKS AND CURRENT LITERATURE

A REVISION OF RHIPSALIS.—There has just appeared an interesting paper[1] which forms the first number of a new botanical serial, Archivos do Jardim Botanico do Rio de Janeiro. It is a great satisfaction that the oldest botanical garden in America, established in 1808, proposes to publish a high grade botanical journal. The garden, itself one of the most beautiful in the world, can very well be made the center for studying the rich flora of Brazil, although it greatly needs an up-to-date herbarium, more botanical reference books, and expert botanists as assistants. This garden is by all means the best place in the world to study palms, where so many species are grown in the open. The new Director, Dr. Pacheco Leao, is to be congratulated in this attempt to make the garden more than a local pleasure park. It is to be hoped that he will receive the proper encouragement from the Department of Agriculture of Brazil, under which the garden is now placed, to make this new venture a success.

Dr. Löfgren for nearly a generation has been engaged in studying the Brazilian flora, chiefly in helping others, having written in this connection but little himself. He contributed much material for use in preparing Brazil's great monument in botany, the Flora Brasiliensis. Dr. Löfgren has spent many years on the genus *Rhipsalis*, of the Cactus family, and is undoubtedly the best informed student of the group now living. The genus itself is a very suitable one to study at the Jardim Botanico do Rio de Janeiro, for this is in the center of its distribution. Of the forty-four Brazilian species, nearly all are to be found in the State of Rio de Janeiro and the adjoining States of Sao Paulo and Minas Geraes. The paper consists of forty-eight pages of text and twenty-five full-page lithographed plates, all beautifully executed. Some of them are not original, being reproduced from plates which appeared in the Flora Brasiliensis and elsewhere.

While we have nothing but praise for Dr. Löfgren's work, we differ from him when he refers *Hariota* (now *Hatiora*) and *Pfeiffera* as subgenera of *Rhipsalis*. It is our opinion also that there are several well

[1] Löfgren, Alberto, O Genero Rhipsalis. Arch. d. Jard. Bot. Rio de Janeiro. 1916.

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defined species now passing under the name of *Hariota salicornioides*, but Löfgren recognizes only two varieties here. *Pfeiffera* does not resemble very closely in its habit, flower or fruit any of the species of *Rhipsalis*, and only on account of its small flowers does it suggest *Rhipsalis*. Dr. Löfgren refers to his subgenus *Pfeiffera* also *Rhipsalis pilocarpa*, on account of its pilose ovary and fruit; but we do not believe it is congeneric with *Pfeiffera* or *Rhipsalis*. In its habit it looks more like *Rhipsalis* proper than *Pfeiffera;* but in its tubular flower, inner perianth segments, style and ovary, is quite different.—J. N. Rose.

Mitosis.—In a recent paper[1] Karsten gives the results of studies on the relation of the frequency of mitosis to light and darkness. He finds that the greater frequencies occur in the dark, both in the root and in the shoot. He finds also a fixed daily periodicity, the maximum number of mitoses occurring between 7 and 11 p. m. Karsten appears to be entirely ignorant of Kellicott's work,[2] done 12 years ago and leading to the same conclusion. The more recent work on the relation of growth to light, temperature and transpiration indicates that any generalizations on the relation between elongation or other extension of growing parts and mitosis, especially when based on the Sachs dictum, quoted by Karsten, is open to criticism.—F. E. Lloyd.

[1] Karsten, G., Über embryonales Wachstum und seine Tagesperiode. Zeitschr. f. bot. **7**: 1-34. 1915.

[2] Kellicott, W. E., The daily periodicity of cell division and elongation in the root of *Allium*. Bull. Torr. Bot. Club 31: 1904.

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NOTES AND COMMENT

The Department of Botany of Stanford University has recently been given control of the arboretum established by Leland Stanford in 1882. A tract of approximately 200 acres was set aside by the founder of the University for the purpose of bringing together "every tree and shrub that would grow in California." Although little planting has been done in recent years the entire tract has been maintained as an arboretum under the management of the Stanford estate. An annual appropriation is to be made for the acquisition of plants, the amount for the current year being $1000. The original collections in the arboretum comprise several hundred species and offer a variety of valuable material for research and class use. The group of plants best represented is the gymnosperms, with 20 genera and 88 species. As it is possible to grow all but the most sensitive cycads out of doors, as well as the northern species of spruce and pine, it should be possible to form a very representative collection of gymnosperms. Dr. LeRoy Abrams, to whom the new development of the arboretum has been entrusted, is endeavoring to bring together as complete a collection as possible of the trees and shrubs of western North America. The assembling of such a group will be of great scientific value and will stimulate the use of our native trees and plants as ornamentals. Coincident with the reorganization of the arboretum the University has set aside as native plant preserves several tracts on its 8000 acre campus. These reserves comprise several natural plant formations, such as stream-bank, oak-madroño, redwood cañon, and chaparral. Undisturbed native vegetation is thereby assured for work in plant ecology. In a preliminary survey of the reserves there have been recorded 64 species of trees and shrubs, representing 29 families.

In the third Technical Publication of the New York State College of Forestry Dr. William L. Bray has described the Development of the Vegetation of New York State. In this paper Dr. Bray has adopted a popular style of treatment which enables him to lead easily from a consideration of the more general aspects of his subjects to a treatment of the most technical features of plant distribution and ecology

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in New York. The clearness and simplicity of the author's exposition bring out the salient features of the geological and physiographic development of the vegetation much better than could have been done if he had attempted to tell us all that he knows about New York vegetation through the medium of the entire ecological vocabulary. Attention has been given chiefly to the distribution of forest trees, and to the sequence of vegetation in bogs and on the sandy areas in various parts of the state. The sub-alpine areas of the Adirondacks, of which so little has been written, are also described. The report is amply illustrated and has a map showing the larger vegetational areas of the state.

Mr. Edward A. Goldman has published the botanical results of an expedition to Lower California made by himself and Mr. E. W. Nelson in 1905 and 1906 (Contributions from the National Herbarium, Vol. 16, Pt. 14). The material is given in the form of a taxonomic list, but so full are the notes on all of the common plants that the paper constitutes a valuable addition to our extremely scanty knowledge of the vegetation of the peninsula and its distributional features. The forty-seven illustrations accompanying the paper are mostly from photographs of individual plants, but they nevertheless serve to portray the character of the vegetation, as well as to show some of the bizarre forms of which it is composed.

Miss Caroline S. Romer has compiled from the notes of the late Dr. Charles Hugh Shaw some of the results of his explorations in the Selkirk Mountains in 1909 and 1910, and published them under the title, The Vegetation of the Selkirks (Botanical Gazette, June, 1916). It is unfortunate that the death of Dr. Shaw, which occurred in the prosecution of his work, has deprived us of the results of the instrumentation which he was carrying out in the Selkirks.

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IMPROVEMENTS IN THE METHOD FOR DETERMINING THE TRANSPIRING POWER OF PLANT SURFACES BY HYGROMETRIC PAPER[1]

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INTRODUCTION

Several features of the method employing cobalt chloride paper[2] for measuring the transpiring power,[3] or coefficient of transpiration, of leaves have recently been considerably improved, and some of these improvements are here presented.[4]

[1] Botanical contribution from the Johns Hopkins University, No. 53.

[2] Stahl, E., Einige Versuche über Transpiration und Assimilation. Bot. Zeitg. **52**: 117–146. 1894. Livingston, B. E., The resistance offered by leaves to transpirational water loss. Plant World **16**: 1–35. 1913. Bakke, A. L., Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecol. **2**: 145–173. 1914. *Idem*, The index of foliar transpiring power as an indicator of permanent wilting. Bot. Gaz. **60**: 314–319. 1915. Shreve, Forrest, The transpiring power of plants as influenced by differences of altitude and habitat. Science, n. s. **43**: 363. 1916.

[3] Transpiring power is the term used by Livingston to denote the ability of the leaf to give off water vapor. It represents the influence of all the internal conditions (effective within the leaf to accelerate or retard transpiration), stomatal conditions being generally important among these. Briggs and Shantz have employed the expression transpiration coefficient in this same sense. (Briggs, L. J., and H. L. Shantz, Hourly transpiration rate on clear days as determined by cyclic environmental factors. Jour. Agric. Res. **5**: 583–650. 1916.) There seems to be no objection to this term, if it is clearly understood that it does not refer to transpiration itself but to one group of conditions (internal ones) that determine the rate of that process.

[4] These improvements are the result of several years of work, to which Miss Aleita Hopping and Mr. E. S. Johnston have contributed, at different times. Miss Hopping's work has been especially important in the early stages of many of the improvements here set forth.

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PREPARATION OF THE COBALT-CHLORIDE PAPER

The usual procedure in the preparation of cobalt chloride paper, simply dipping it in the salt solution and then suspending to dry in the room or drying in an oven on a glass plate, has proved unsatisfactory; this procedure gives papers that are not at all uniform, and uniformity of paper is greatly to be desired.

Munktell's Swedish filter paper, number 00, was recommended by Bakke for this purpose, but only a small percentage of the sheets, as furnished by dealers, can be used, most of them varying too much in thickness. Whatman filters no. 30 (11 cm. circles) have been finally adopted, this proving to be somewhat better than the other, in our tests.

The cobalt chloride solution used contains 3 grams of the salt (dried at 110°C.) in 100 cc., and is made distinctly acid by addition of a little hydrochloric acid. The dry paper is placed in the solution and the vessel is agitated for one minute; during this process the sheet is turned several times. It is then placed on a clean glass or ferrotype plate and the excess of solution is squeezed out with a photographer's squeegee roller, of rubber. Then a piece of clean, dry blotting paper is laid upon it and the rolling is repeated, with considerable pressure. Next the circle of paper is partly dried in an oven, between two pieces of blotting paper, but it must not be dried to the blue color. While still pink it is removed from the oven, placed between two sheets of clean filter paper, on a smooth surface, and thoroughly dried by heat and pressure, applied by an electric flatiron. When the sheet is thoroughly dry the blue color is compared with the more intense of the two color-standards to be described below. To be acceptable, the blue of the cobalt chloride paper must be distinctly more intense than that of the standard. The intensity of color may be varied by altering the length of the time period during which the paper remains in the solution, which seems more satisfactory than changing the concentration of the solution.

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THE USE OF PERMANENT COLOR-STANDARDS

As this general method has been heretofore employed, the cobalt-chloride paper slip is dried, usually by the application of heat, quickly placed upon the leaf to be tested and then covered with a glass or mica plate. The time period required for the color change is considered as beginning when the slip is placed upon the leaf. There is considerable variation, however, in the amount of time required to transfer the slip from the position where it has been dried to the leaf, and the amount of moisture taken up by the paper during this short interval must vary with the length of the interval, as well as with the pressure of water-vapor in the air at the time. It is certain that every hygrometric slip takes up *some* moisture during this transfer, and the amount thus taken up is not always the same, thus introducing a variation in the moisture content of the slip when the test is begun. To correct for such variations is practically impossible, and they frequently introduce a serious error, especially when the air is moist, when the transfer is made slowly, and when the leaf surface in question has a high transpiring power. We may term this the *initial* error in the operation.

When a test is finished its termination is shown by the attainment of a certain color by the paper slip. The end point of the color change is taken as that point at which the test slip has the same color (pale pink) as that of an originally similar slip placed upon the same kind of leaf some time previously. Or else, the test is considered as ended when blue color can no longer be detected, this end point being less definite than the one obtained with the control slip just referred to. Considerable variations in color judgments are frequently introduced by both these methods, resulting in a corresponding error in the determination of the end point of color change. This may be termed the *final* error.

To reduce both of these errors as much as possible a method employing two permanent standard colors has been devised. These colors are both blue, one of them being a little less intense than is the color of the thoroughly dry cobalt-chloride

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paper, while the other is much less intense than that, but nevertheless clearly and unquestionably blue. By means of the composite slips to be described below, these two permanent color standards are brought to the leaf surface simultaneously with the hygrometric slip itself, and closely alongside it. When the slip is dry it is more intensely blue than the more intense one of the color standards. During the process of transfer to the leaf surface and while the glass plate is being applied this color gradually decreases in intensity, until, some time (a few seconds) after everything is arranged, the color of the hygrometric paper just matches in intensity the more intense standard.

The test is not actually begun until this point of the color change is reached, so that this improvement allows the transfer and the placing of the glass plate to consume a little more time than would be thought allowable by the old method. A difference of a very few seconds in the time allowed for these operations is sufficient to determine whether they may be performed in a truly efficient manner or whether they must be hurried. Undue haste in trying to place the hydrometric slip before it will have altered its moisture content "too much" has doubtless caused many a miscarriage in the beginning of a test.

Aside from this feature of avoiding undue haste in placing of the slips, this initial color standard greatly decreases the uncertainty regarding their moisture content at the moment when the test is actually begun. By the old method, even if the transfers always consumed exactly the same amount of time, variations in air humidity were still effective to produce an unknown variation in the initial moisture content. Whether a test is performed with high or low air humidity now makes no difference, for the initial color standard is so chosen that even very humid air does not cause the color change to occur so rapidly but that time is amply allowed for all the necessary operations, before the color of the slip comes to match that of the initial standard. Thus most of the initial error is obviated.

The other permanent color standard is employed to avoid the final error, in a similar way. The color of this standard is a very pale blue, of such quality and intensity that the color

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of the cobalt-chloride paper, as the latter absorbs moisture, comes to have just the same intensity as the color standard. This occurs appreciably before all blueness disappears from the cobalt-chloride slip. A test is considered as ended when the slip just matches the color of this less intense standard. Since the two color standards are permanent in color, they furnish two fixed points in the series of color intensities that are presented as the test paper alters from intense blue to pink, and the test now becomes, simply, to determine the length of time elapsing between the occurrence of a fixed strong intensity of color and that of an equally fixed weak intensity. This modification has been found to decrease the final error, in determining the end point, to a marked degree.

PREPARATION OF THE PERMANENT COLOR STANDARDS

The color standards are made by precipitating Prussian blue in filter paper of the same kind as is used for preparing the cobalt-chloride paper. This precipitation is affected by bringing ferric chloride and potassium ferrocyanide together in the paper; if the pigment is formed in the solution outside of the paper it has been found impossible to cause it to enter uniformly afterwards. The paper is first impregnated with ferric chloride, by immersing for the proper time in a solution of this salt, of the proper concentration, and the excess of solution is then removed, first by means of the rubber roller alone and finally by means of roller and clean blotting paper. Next, without further drying, the paper is placed in a properly concentrated solution of potassium ferrocyanide and allowed to remain there for the proper time, after which it is dried with roller, with roller and blotting-paper, and finally with hot electric flatiron and blotting paper. If the solutions have the correct concentration, if the paper is left for the right length of time in each one, if the blotting paper used is clean and fresh for each application, and if numerous other details are properly carried out, the resulting paper has the correct quality and intensity for the color standard.

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Since ferric chloride is extremely hydroscopic and since it cannot be dried to constant weight without undergoing decomposition, it is impossible to give explicit directions for preparing the solutions of this salt. The proper concentration is to be obtained by means of preliminary tests (in the actual preparation of filter paper circles). This concentration might have been determined by analysis, but this was thought unnecessary, since practical tests must be resorted to in any event. The ferric chloride solution used by us for the more intense color standard contained about 2.28 g. of the undried salt (of unknown water-content) in 100 cc. The solution used for the less intense standard contained about 0.13 g. in 100 cc. These solutions must be made distinctly acid, by addition of hydrochloric acid.

Since potassium ferrocyanide may be dried to constant weight, the concentrations used for our solutions of this salt may be definitely stated. The solution employed in preparing the more intense color standard contained 36.8 mgm. of dry salt in 100 cc., and the one for the less intense standard contained 5.3 mgm. in 100 cc. It is needless to remark that all the concentration actually used, for both salts, were obtained by diluting much more concentrated solutions.

The procedure followed is somewhat complicated and the operator requires much practice before perfect pieces of the permanently blue paper may be produced with assurance. The paper circle is first placed in distilled water for one minute, being reversed once. Then it is squeezed by means of the roller on a ferrotype plate. The roller is passed over it in two directions, at right angles to each other. Next, a fresh piece of blotting-paper is laid over the circle as it rests on the plate, and the double rolling is repeated, the blotting-paper being renewed for the second rolling. The uniformly moist sheet thus obtained is now placed in the proper solution of ferric chloride, where it remains for from one to two minutes (more intense standard) or from ten to fifteen seconds (less intense standard), according to the temperature. (At 20°C. one minute was sufficient, at 16°C. two minutes were required, for the more intense stand-

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ard.) The solution, 100 cc. in a glass pan somewhat larger in diameter than the diameter of the filter-paper circle, is agitated during the entire treatment and the sheet is reversed once. Next follows double rolling on the ferrotype plate, with the bare roller and with blotting-paper interposed, the latter being again renewed between rollings. There once more results a uniformly moist sheet of filter paper, which is now placed in the proper solution of potassium ferrocyanide. Here it remains for the same time as in the case of the ferric chloride solution, for the more intense color, and from fifteen to twenty seconds, for the less intense. Upon being removed from this solution the sheet is once more subjected to double rolling on the plate, and to another double rolling with blotting-paper interposed (the latter once more renewed between the two rollings). Finally, the circle is placed between two fresh sheets of dry blotting-paper and thoroughly dried by means of the hot electric flatiron.

Each finished sheet is compared (after cooling) with a standard sheet of the proper intensity of color, and is discarded if any difference in color can be detected. The final intensity of color may be altered by altering the time during which the circle remains in the ferrocyanide solution, by altering the temperature, or by altering the concentrations. A chemical excess of ferrocyanide is always to be used. After a number of circles have been treated the solutions are renewed.

The colored papers thus prepared are found to be permanent; at least they do not alter their color when exposed to air and sunshine for several days, and they do not alter their color with changes in hydroscopic moisture, such as are obtained when they are placed over the standard evaporating surface or upon a leaf. The rather great labor and expense of preparing them are offset by the fact that but little paper is required to make a very large number of slips of the proper size for leaf tests.

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COMPOSITE PAPER SLIPS

In order to bring the cobalt paper slip and those of the two color standards into juxtaposition, and to allow the three to be readily handled in use, a method has been worked out by which they are firmly joined together into a single composite slip, which can be manipulated as a single piece. It is obviously not permissible to join the three pieces by overlapping and pasting, nor should any other material be pasted over the lines of junction on the surface that is to absorb water. However, on the surface from which observations are made the lines of junction may each be covered by a very narrow strip of thin, non-absorbent material. For this purpose black silk court-plaster has been successfully employed. Each black strip is 1 mm. wide, and covers the line where the two papers adjoin, thus fastening them together.

In the making of these slips it is found convenient first, to cut the cobalt paper and the permanent blue papers into strips 4.5 mm. wide, and about 6 or 8 cm. long. The cobalt strip is laid upon clean glass, a permanent blue strip being laid against each of its long edges, and a court-plaster strip carefully cemented over each of the two lines of marginal contact. Across the composite strip, thus resulting, similar strips of court-plaster are then cemented in a horizontal direction at intervals of 4 mm. After drying between sheets of writing paper, under pressure, these composite strips are cut cross-wise through the center of the horizontal strips of court-plaster, thus producing the finished composite strips, each one being about 9 mm. long and 5 mm. wide. Each of the three paper surfaces visible to the observer when the strip is in use is about 4 mm. square, and is surrounded by a black frame 1 mm. wide. It is found in practice, that these composite slips may be handled in the same manner as are the simple ones. By this arrangement the two standard colors are automatically placed in position whenever the cobalt slip is applied to any surface to be tested. Of course the standard papers absorb moisture, but their colors are not thereby altered, while the cobalt chloride piece changes from deep blue to nearly white.

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THE DRYING OF THE SLIPS

The composite slips may be dried either by heat or by means of a desiccator. If heat is employed some form of desiccator is necessary to retain them in the dry condition until they are used and to bring them to air temperature in the dry state. It has been found convenient to arrange a number of tiny desiccators, each to hold a single slip, or perhaps two, and to open these one after another as the slips go into use. Very small opal-glass salve jars, fitted with rubber stoppers, have been found satisfactory for this purpose. They are nearly filled with anhydrous phosphoric acid, which is covered with a circle of fine wire gauze, the paper slip being placed upon the gauze and the stopper forced in tight. Thus the slips remain in the dry condition indefinitely.

In laboratory work an electric hot-plate is found valuable for quickly drying the slips; an inverted electric flat-iron is excellent. A metal plate heated by a very small flame is also suitable. In any case, heating should be controlled so as not to injure the paper. Twenty-four hours of continuous heating even at 100°C. will char the paper enough to spoil the colors, and as this effect is doubtless cumulative it is advisable to heat the slips no longer than the few seconds required to change the cobalt paper to a shade more intensely blue than the more intense of the standard colors.

THE STANDARD EVAPORATING SURFACE

One of the main difficulties encountered in the operation of hygrometric paper tests has heretofore been related to the arrangement of the standard evaporating surface. This apparatus has received considerable attention during the progress of our studies, and many different forms have been devised and discarded. The most satisfactory form yet tried by us, will now be described.

The evaporating surface itself is of porous clay, like that of

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the ordinary atmometer cup.[5] This particular kind of cup serves very well here, but needs to be ground off at the closed end so as to form a flat surface somewhat over 1 cm. in diameter and perpendicular to the long axis of the cup. If the grinding be too long continued the end wall of the cup will of course be completely removed, but this wall is sufficiently thick to allow the formation of the small plane surface here required.

An opening about 8 mm. in diameter is drilled in the side of the cup, about 1 cm. from the closed end, and a thermometer bulb inserted, with a small rubber stopper. It is well if this thermometer has a bent stem, the scale portion being vertical and about 7 cm. distant from the horizontal bulb, which is within the cup. The whole outer surface of the cup excepting the flat top is thoroughly waterproofed with shellac or melted sulphur, to prevent water loss anywhere except through the plane surface at the top.

The upper portion of the cup is now set into the center of a piece of wood about 10 cm. square and 2 or 3 cm. thick, so that the plane top of the wood block is continued at the center by the flat porous clay plate formed by the top of the cup (see figure 1). The cup is held in place by sealing-wax or a similar cement. It is best not to finish grinding the porous surface until the cup is in place, and to fix the latter so that the top projects a little above the wood surface. The projecting portion of porous clay is afterwards removed by grinding, and the entire surface (of wood and clay) is made plane.

The horizontal part of the thermometer is set into a suitable groove in the lower side of the wood block. A rubber tube is placed about this portion of the stem, and then the groove is filled with wax cement, to retain the thermometer in place. The whole wood block is heavily water-proofed with shellac.

To provide the millimeter of vapor blanket so far used over the standard evaporating surface, a plane sheet of metal, hard

[5] Livingston, B. E., The relation of desert plants to soil moisture and to evaporation. Carnegie Inst. Wash. Publ. 50. Washington. 1906. Atmometry and the porous cup atmometer. Plant World 18: 21–30, 51–74, 95–111, 143–149. 1915. Also reprinted, Tucson, 1915.

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rubber or pressed fiber of this thickness, and with a rectangular opening at its center, 4 x 8 mm., is placed upon the upper surface of the wood block, the opening lying over the exposed porous surface. A glass plate overlies this, covering the cobalt paper slip in the manner heretofore used with the Harvey blotting-paper surface.[6] The millimeter plate may be attached to the wood if this seems desirable, but it should not be allowed to buckle with rise in temperature. A good way to attach it is by means of four thumb-tacks placed outside of its margin, near the corners.

The porous cup is filled with distilled water and mounted as with the ordinary absorbing mounting of the atmometer.[7] The glass tube is only about 8 cm. long here, however, and the small reservoir bottle is brought as close as possible to the porous cup. Care should be exercised in filling to have no air-bubbles in the cup. The complete apparatus is conveniently supported on a small tripod ring, the bottle hanging below the wood block, which rests upon the ring.

The apparatus just described furnishes a suitable standard evaporating surface for laboratory and greenhouse use, but is not convenient for the field. The temperature to be considered in the operation of this instrument is the temperature of the evaporating surface itself and the placing of a glass and mercury thermometer so as to give readings of this temperature is difficult or impossible. The temperature determined by means of the thermometer in the apparatus just described is not precisely that of the evaporating surface; it is simply the temperature of the mass of water that bathes the porous clay plate from within the cup. It is thus seen that the instrument here recommended for laboratory and greenhouse is not quite perfect in this particular; there is room for improvement.

For field use, it is inconvenient to employ any arrangement of the standard evaporating surface that has a thermometer as an essential part. During the years when the use of standardized cobalt-chloride paper has been developing, many differ-

[6] See Livingston, 1913, *l.c.*

[7] See Livingston, 1915, *l.c.*

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ent types of this apparatus for the field have been devised, but they all agree in the absence of any means for determining the temperature of the evaporating surface, or even of the water behind that surface. Perhaps the most convenient form of evaporating-surface apparatus is that devised by Bakke,[8] which is a much improved form of the original Harvey instrument.[9] We understand that this type of instrument is to be placed upon the market.

A somewhat less convenient but less expensive form of this apparatus, has been developed in our own work. It is a simple modification of the laboratory form above described. A small porous clay cup (about 2 cm. in diameter and 5 or 6 cm. long) is set into a flat cork stopper just as the larger one is set into a block of wood, the top of the cup being ground flat to coincide with the upper surface of the stopper. Over this surface is cemented a piece of hard rubber 1 mm. thick, with an opening over the porous plate, as in the other form. This rubber plate is trimmed at its margins to the size of the stopper. The latter fits a large-mouth bottle of squat form (to avoid its being upset too readily) and the porous cup extends into the bottle nearly to the bottom. The bottle is nearly filled with distilled water, the cup and stopper are put into place, and the whole is then inverted. This expels the air from the cup, and when the instrument is again placed upright the cup remains filled with water, as in the larger form. Aside from the fundamental objection arising from somewhat uncertain temperatures of the evaporating surface, this type of instrument has proved very satisfactory.

TEMPERATURE RELATIONS OF RATE OF COLOR CHANGE IN COBALT-CHLORIDE PAPER

As has been well pointed out by Bakke, the only condition outside of the hygrometric paper itself, that can be influential in determining the time period required for its color change

[8] Bakke, A. L., and B. E. Livingston, Further studies on foliar transpiring power of plants. Physiol. Res. **2**: 51–71, 1916.

[9] Livingston, 1913, *l.c.*

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over the standard evaporating surface, is temperature. With the same paper slip and the same evaporating surface, a higher temperature should give a shorter time of response than does a lower temperature. "On theoretical grounds it is to be expected that the relation here brought out is simply the well-known relation which holds between temperature and the vapor-pressure of water."[10] Bakke has presented experimental evidence which appears to show that the relation here dealt with is approximately linear for the temperature range from 25° to 35°C. and that the graph of this relation becomes concave upward with higher temperatures. The same writer suggests that, if this temperature relation can be satisfactorily established, the standard evaporating surface may be dispensed with in field work, each hygrometric slip having been tested once for all, in the laboratory, at a known temperature. From the observed time of response at the known laboratory temperature and from the field temperature when leaf tests are made, it should thus be possible to calculate the time of response for the field temperature, as though the paper had there been tested over the same standard surface as was used in the laboratory.

It appears probable[11] that the temperature relation here in question may be expressed by the statement that the time of color response is inversely proportional to the maximum vapor pressure of water corresponding to the temperature. This pressure varies with temperature in a known way (empirically determined), and its value may be found from published tables, for any given temperature. This supposition may be familiarly stated as follows:

$$\frac{p}{P} = \frac{R}{r}, \text{ or } pr = PR, \text{ or } r = \frac{PR}{p},$$

wherein P is the maximum vapor-pressure corresponding to the temperature at which the actual test was carried out with the

[10] Bakke, 1914, p. 150, *l.c.*

[11] See Trelease, S. F., and Livingston, B. E., The daily march of transpiring power as indicated by the porometer and by standardized hygrometric paper. Journ. Ecol. **4**: 1, 1916.

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standard surface, p is the corresponding maximum vapor-pressure for the given field temperature, R is the time of response observed in the laboratory (with maximum vapor pressure P), and r is the calculated time of response for the field temperature.

According to this argument, the time required for color change of a slip of paper over the standard surface at temperature t' may be calculated from the corresponding time required by the same paper over the same surface at temperature t. These times may be called R_t and R_t' (R and r in the formula just given). We find (from tables) the maximum vapor-pressure of water in the air for temperatures t and t' (which may be called P_t and P_t, which are P and p above) and then apply the formula,

$$R_{t'} = \frac{P_t\, R_t}{P_{t'}}.$$

Thus if a slip required 45 sec. to change over the standard surface at 20°C. (vapor-pressure, 17.36 mm. of mercury), the time required at 25°C. (vapor pressure, 23.52 mm.) would be

$$R_{t'} = \frac{17.36 \times 45}{23.52} = 33.2 \text{ sec.}$$

The temperature t should be a function of the temperatures of the evaporating surface of the rubber plate, and the glass plate covering the paper slip, but if the apparatus has been exposed for some time in the place where the test is made, it appears safe to consider that the temperature of the water just behind the plate (as indicated by the thermometer in the laboratory type of apparatus) is a measure of the temperature influence in question. In testing slips in the laboratory, it is advisable to keep the glass plate over the apparatus at all times except when it is momentarily removed to place a slip. This practically prevents a lowering of the temperature of the evaporating surface through evaporation, and the whole apparatus assumes approximately air-temperature. Such tests should be made with air-temperature maintained as nearly constant as possible.

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It should also be emphasized that, in this connection, the whole method of standardized hygrometric paper slips, as so far used, is based on the supposition that the papers lying upon plant leaves are under the influence of the temperature of the air about the plant. As Trelease and Livingston[12] have pointed out, this is probably never quite the case, and as soon as leaf temperatures can be measured conveniently it will be necessary to employ these readings (as t') instead of those taken on a thermometer simply exposed beside the plant or among its leaves. Even such a procedure as this may eventually require correction, for the temperature influence exerted upon a slip lying upon a leaf and covered by a glass plate must be determined by the temperatures of leaf and plate together. For the present it seems sufficient to consider that the surrounding air temperature is a measure of the temperature influence exerted upon the paper slips when lying upon plant leaves.

During the summer of 1914, Miss Aleita Hopping, working at the Laboratory of Plant Physiology of the Johns Hopkins University, made a large number of determinations of the response times for a series of selected composite slips, at various air-temperatures, from 19.4° to 41.7°C., the same form of evaporating surface being used in all cases. Although the methods employed were not as satisfactory as those set forth in the earlier sections of the present paper, and although the paper employed at that time was much thinner than that now used (thus having a much shorter time coefficient), nevertheless the results obtained definitely support the suppositions just presented and appear worthy of expression here.

Thirty tests were made at a temperature of 24.8° C. and the average time of response was calculated, all of the slips in the series giving about the same value. Tests were then made at various different temperatures, as the air of the room varied from time to time, until a considerable number of observations had been obtained for each temperature dealt with. The response times for each temperature were then averaged and this

[12] Trelease and Livingston, 1916, *l.c.*

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average was compared with the theoretical response time for that temperature, as calculated from the average of 30 tests at 24.8°C. The results obtained, together with the corresponding calculated and experimentally derived values, are given in table 1.

TABLE 1

Time periods required for color change of hygrometric paper slips over standard evaporating surface at various temperatures as obtained experimentally and as calculated from the period required at 24.8°C. All tests at each temperature are represented by a single average

TEMPERATURE	NO. OF TESTS MADE	MAXIMUM VAPOR-PRESSURE* OF WATER	AVERAGE OF OBSERVED TIME PERIODS	TIME PERIOD CALCULATED FROM THE AVERAGE FOR 24.8°	VARIATION OF CALCULATED FROM OBSERVED VALUE	
					Arithmetical	Geometrical
deg. C.		*mm.*	*sec.*	*sec.*	*sec.*	*per cent*
19.4	13	16.776	23.3	23.7	+0.4	+1.7
20.8	25	18.278	21.3	21.6	+0.3	+1.4
22.2	6	19.900	20.0	19.9	−0.1	−0.5
22.7	16	20.510	19.4	19.3	−0.1	−0.5
22.8	31	20.634	19.3	19.2	−0.1	−0.5
23.8	30	21.913	18.5	18.0	−0.5	−2.7
24.4	22	22.716	17.5	17.4	−0.1	−0.6
24.8	30	23.266	17.0	——	——	——
25.4	35	24.113	15.8	16.4	+0.6	+3.8
26.4	12	25.584	15.5	15.5	——	——
27.3	22	26.976	14.3	14.7	+0.4	+2.8
28.0	70	28.103	13.5	14.1	+0.6	+4.4
29.5	10	30.659	12.8	12.9	+0.1	+0.8
30.3	41	32.103	12.6	12.3	−0.3	−2.4
30.6	11	32.660	12.2	12.1	−0.1	−0.8
31.0	32	33.416	11.5	11.8	+0.3	+2.6
32.8	26	37.008	10.3	10.7	+0.4	+3.9
34.4	26	40.479	9.6	9.8	+0.2	+2.1
38.5	28	50.610	7.0	7.7	+0.7	+10.0
41.7	39	60.060	6.3	6.6	+0.3	+4.8

* "According to Regnault, Broch and Weibe," as given in Van Nostrand's chemical annual, edited by J. C. Olsen, 2d issue; New York, 1909. (Table lxxix, p. 436.)

From the percentage variations in the last column of table 1 it is seen that the averages derived from direct observations and the values calculated from the average for 24.8° are generally in exceedingly good agreement. It is frequently found that

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tests on plant leaves show unexplained variations of several per cent. On the whole, it may be concluded, that the time period for a slip at any given temperature may be as satisfactorily obtained by calculation from the observed period at another temperature, as by actual tests made at the given temperature. Indeed, it is practically certain that calculations for field temperatures, made from the average of a large number of tests in the laboratory, will prove to be more nearly correct than most single field tests, or even averages of a number of the latter; these tests can be carried out more easily and with greater precision in the laboratory than is usually possible in the open.

PERMANENT STANDARDIZATION OF THE PAPER SLIPS

Considering that the simple temperature relation dealt with in the last section may be regarded as established, it follows that the testing of the paper slips in the field may now be generally dispensed with, thus doing away with the need of a convenient field instrument for this test. Each composite slip is to be thoroughly tested in the laboratory, under known temperature conditions, and from the average time period derived from a number of such tests a correction coefficient is to be calculated for each temperature at which field observations are to be carried out. The standard evaporating surface is not to be taken to the field at all.

Using the porous cup apparatus first described in this paper, it is not a very arduous task to make a large number of determinations upon each single composite slip. The slips are first numbered on a corner of the under surface of the more intense blue standard (that is, on the side which lies against the leaf in actual use, the side on which no black bars are visible). Records are kept by slip numbers, as the tests are made, and, finally the average time period for color change of that particular slip at 20°C. is found by calculation, and is expressed as a single number characteristic of that slip. Knowing this number and also the air temperature at which any field test is being made, the time period for this slip at the latter temperature (on the

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standard evaporating surface) may be readily found by employing a table of aqueous vapor-pressures and the formula for r_t' given above.

It will be seen at once from the formula that

$$R_{t'} = R_t \times \frac{P_t}{P_{t'}}$$

Now, R_t (which is R_{20} when 20° is taken as standard temperature) is a characteristic constant for any slip of paper, to be found by looking up the slip, by its number, in the standardization record. P_t is 17.406 mm.,[13] and $P_{t'}$ may be found from a table of vapor-pressures, being the vapor pressure corresponding to the field temperature with which the leaf tests are being made.

As in other similar cases, it is convenient to calculate the ratio $\frac{P_t}{P_{t'}}$ for all the temperatures for which it may be needed and to arrange these values in the form of a table for field use. Our table 2 is such a table of ratios, for all temperatures from 0° to 45.9°C., by increments of 0.1°. From the nature of their derivation, each of the values here given is a coefficient of correction by which must be multiplied the characteristic time period at 20° (R_t), for any slip of paper, in order to obtain the corresponding time period for the same slip of paper (on the standard evaporating surface) at the temperature to which the coefficient refers. Following the usual custom in such cases, whole degrees of temperature are shown in the first column of table 2 and the added tenths are shown at the heads of the other columns. Thus, the coefficient for 15.0° is 1.37, that for 15.4° is 1.34, that for 20.0° is 1.000, that for 21.6° is 0.91, etc. The vapor-tensions for these calculations have been taken from Broch's table, as given in the Smithsonian meteorological tables,[14] and the values are slightly different from those employed for our table 1.

[13] From Van Nostrand's chemical annual, 1909.

[14] Smithsonian meteorological tables, 3rd revised edition. Smithsonian Institution, Washington, 1907. Table 43, which is from "Broch, Trav. Mem. Bur. Internat. Poids et Mesures 1: A19–39."

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TABLE 2

Ratios of maximum vapor pressures of water in the air at 20°C. (17.36 mm.) to the corresponding pressures at temperatures from 0° to 45.9°C., by increments of 0.1°

$R_t = \frac{P_{20}}{P_t} R_{20}$ — R_t = TIME AT t'°. P_t' = VAPOR PRESSURE AT t'°. P_{20} = VAPOR PRESSURE AT 20°. NUMBERS GIVEN BELOW ARE $\frac{P_{20}}{P_t}$

t' DEG. C.	0	.1	.2	.3	.4	.5	.6	.7	.8	.9
0	3.80	3.77	3.74	3.72	3.70	3.66	3.64	3.62	3.59	3.57
1	3.54	3.51	3.48	3.46	3.44	3.41	3.38	3.36	3.34	3.32
2	3.29	3.27	3.24	3.22	3.20	3.18	3.16	3.13	3.11	3.09
3	3.07	3.05	3.02	3.00	2.98	2.96	2.94	2.92	2.90	2.88
4	2.86	2.84	2.82	2.80	2.78	2.76	2.74	2.73	2.71	2.69
5	2.67	2.65	2.63	2.61	2.59	2.58	2.56	2.54	2.52	2.51
6	2.49	2.47	2.46	2.44	2.42	2.41	2.39	2.38	2.36	2.34
7	2.32	2.31	2.29	2.28	2.26	2.25	2.23	2.22	2.20	2.19
8	2.17	2.16	2.14	2.13	2.12	2.10	2.09	2.07	2.06	2.05
9	2.03	2.02	2.00	1.99	1.98	1.97	1.95	1.94	1.93	1.91
10	1.90	1.89	1.87	1.86	1.85	1.84	1.83	1.81	1.80	1.79
11	1.78	1.77	1.75	1.74	1.73	1.72	1.71	1.70	1.69	1.68
12	1.66	1.65	1.64	1.63	1.62	1.61	1.60	1.59	1.58	1.57
13	1.56	1.55	1.54	1.53	1.52	1.51	1.50	1.49	1.48	1.47
14	1.46	1.45	1.44	1.43	1.42	1.42	1.41	1.40	1.39	1.38
15	1.37	1.36	1.35	1.34	1.34	1.33	1.32	1.31	1.30	1.29
16	1.28	1.28	1.27	1.26	1.25	1.24	1.24	1.23	1.22	1.21
17	1.21	1.20	1.19	1.18	1.18	1.17	1.16	1.15	1.14	1.14
18	1.13	1.13	1.12	1.11	1.10	1.10	1.09	1.08	1.08	1.07
19	1.06	1.06	1.05	1.04	1.04	1.03	1.02	1.02	1.01	1.01
20	1.00	.99	.99	.98	.98	.97	.96	.96	.95	.95
21	.94	.94	.93	.92	.92	.91	.91	.90	.90	.89
22	.88	.88	.87	.87	.86	.86	.85	.85	.84	.84
23	.83	.83	.82	.82	.81	.81	.80	.80	.79	.79
24	.78	.78	.77	.77	.77	.76	.76	.75	.75	.74
25	.74	.73	.73	.73	.72	.72	.71	.71	.70	.70
26	.70	.69	.69	.68	.68	.68	.67	.67	.66	.66
27	.66	.65	.65	.64	.64	.64	.63	.63	.63	.62
28	.62	.61	.61	.61	.60	.60	.60	.59	.59	.59
29	.58	.58	.58	.57	.57	.57	.56	.56	.56	.55
30	.55	.55	.54	.54	.54	.53	.53	.53	.53	.52
31	.52	.52	.51	.51	.51	.51	.50	.50	.50	.49
32	.49	.49	.49	.48	.48	.48	.48	.47	.47	.47
33	.46	.46	.46	.46	.45	.45	.45	.45	.44	.44
34	.44	.44	.43	.43	.43	.43	.42	.42	.42	.42
35	.42	.41	.41	.41	.41	.40	.40	.40	.40	.40
36	.39	.39	.39	.39	.39	.38	.38	.38	.38	.37
37	.37	.37	.37	.37	.36	.36	.36	.36	.36	.35
38	.35	.35	.35	.35	.36	.34	.34	.34	.34	.34
39	.33	.33	.33	.33	.33	.33	.32	.32	.32	.32
40	.32	.31	.31	.31	.31	.31	.31	.31	.30	.30
41	.30	.30	.30	.30	.29	.29	.29	.29	.29	.29
42	.28	.28	.28	.28	.28	.28	.28	.27	.27	.27
43	.27	.27	.27	.27	.26	.26	.26	.26	.26	.26
44	.26	.25	.25	.25	.25	.25	.25	.25	.25	.24
45	.24	.24	.24	.24	.24	.24	.24	.23	.23	.23

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Table 2 is also employed in the standardization calculations when the room-temperature where the tests are made (or the water-temperature) is not 20.0°, but in this case the coefficient given in the table is considered as inverted, and its reciprocal is employed. For example, if a given slip is tested at 19.5° and is found to have a period of change of 50 sec. (between the times when it matches the more intense and the less intense color standard, over the evaporating surface), the number 50 is divided by the coefficient for 19.5° (1.03, from table 2), to give 48.5, the calculated time period for 20.0°.

To illustrate the use of table 2 in connection with leaf tests, a certain slip, with a time period of 44 sec. at 20.0°, is applied to a leaf when the air temperature near that leaf is 30.3°, the thermometer being shaded from solar insolation, as is also the leaf during the test. It is found that color change occurs in 3 min. or 180 sec. We now find from table 2, that the coefficient for 30.3° is 0.54, and we multiply 44 by this quantity, thus obtaining 23.76 sec. the calculated time period for the slip over the standard evaporating surface at 30.3°. Finally, we divide 23.76 by 180, to obtain the index of transpiring power of the leaf surface tested, which is found to be 0.13.

Slips may be standardized and used repeatedly, so long as they are kept clean and free from color changes caused by slight charring. Of course they must not be touched with the fingers; a pair of clean, dry forceps is always employed for handling them. If a slip becomes wet with liquid water or with any exudation from the plant, or if it is otherwise soiled, it is to be discarded.

RANGE OF APPLICABILITY OF THE SLIPS

It is obvious that any method depending for its results upon a rate of change, is applicable only with a range of conditions that allow the change dealt with to go on at a measurable rate. In the present connection, the transpiring power of plant surfaces cannot be determined by means of hygrometric paper unless these surfaces do give off moisture to the dried slips with considerable rapidity, and unless this movement of moisture

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continues until the color of the cobalt-chloride paper is altered beyond the point where it matches the color of the less intense standard. The rate of color-change thus brought about must be great enough so that lateral leakage of moisture into the hygrometric slip (from the air outside or from other parts of the surface not covered by the slip but covered by the glass plate) shall be practically negligible. At the same time, surfaces that give off water too rapidly cannot be studied in this way, for in such cases the rate of color-change becomes too rapid to be measured.

The water reaching the slip must be vapor and not liquid; leaves whose surfaces are wet with liquid water (as rain or dew) cannot be dealt with by this method.

The difficulty arising from the fact that certain plant surfaces give off moisture at a rate too slow to be studied by this means may be a far more serious one, being encountered with at least one of the two surfaces of certain extremely xerophilous leaves. Thus, Livingston (1913) was unable to determine the transpiring power of the upper surfaces of leaves of *Rhus acromatica* because the paper slips he employed upon these surfaces failed to complete their color changes.[15] Such difficulties may sometimes be overcome by adopting a more intense blue as the weaker color-standard. In other cases a thinner paper may be employed, but in any event such cases require special attention.

As has been mentioned, the hygrometric paper employed in our later studies, the one for which the two permanent color standards have been developed, is much slower in its color reaction than that used earlier, by Bakke and by ourselves. At 20°C. it requires about 45 seconds (41–48) for response on the standard evaporating surface, with a gas layer a millimeter thick between paper and porous plate. Plant surfaces to be studied by means of this paper should show periods between about 15 or 20 seconds and perhaps an equal number of minutes.

[15] It may be mentioned here that Livingston's statement regarding the comparative transpiring powers of *Sphaeralcea* plants growing at Oracle and on the Desert Laboratory grounds (page 31) is transposed; it was of course those at the Laboratory (lower station) that exhibited the lower indices, as is shown by his table 6.

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To illustrate the range that may be met with in different plants the following series of tests were carried out, upon various different physiological types of plants that happened to be available at the time the physical and chemical portions of this study had been completed. Corresponding tests with the standard evaporating surface were not carried out, our aim being simply to obtain an idea of the actual experimental time periods required by the new paper and by the different plants considered. The plants were growing in the greenhouse. A number of tests were carried out upon each plant, and the series of values given in each case represent different tests.

Duranta plumieri (27°C., bright sunshine, 1:20 p.m.). Different leaves of same apparent age and size, lower surface: 50, 72, 58, 43, 61, 43, 43, 47, 40, 50 sec.

Coleus blumei (20°C., bright sunshine, 3:20 p.m.). Young, immature leaves, lower surface: 150, 150 sec. Young, adult leaves, lower surface: 65, 90, 100 sec. Older adult leaves, lower surface: 181, 150 sec. Young, adult leaves upper surface: 900, 900 sec.

Ficu elsastica (27°C., bright sunshine, 2:15 p.m.). Different leaves apparently alike, lower surface: 67, 70, 90, 90, 90 sec. Upper surface: 540, 420, 540 sec.

Ficus pandurata (27°C., bright sunshine, 11:30 a.m.). Different parts of same mature leaf, lower surface: 145, 150 sec. Different parts of younger leaf, lower surface: 145, 155 sec.

Albizzia saman (28°C., bright sunshine, 11:50 a.m.). Different leaves, apparently alike, lower surface: 20, 25, 25, 25, 25, 20 sec.

Yucca aloifolia (20°C., bright sunshine, 12:10 p.m.). Different leaves, apparently alike, lower surface: 400, 310 sec. Upper surface: 234, 224, 274, 264 sec.

Pelargonium zonale (24°C., bright sunshine, 3:00 p.m.). Different leaves, apparently alike, lower surface: 33, 30, 33 sec. In shade: 70, 150, 160 sec. Upper surface: 175, 150, 160 sec.

Bryophyllum calycinum (24°C., weak sunshine 4:00 p.m.). Different leaves, apparently alike, lower surface: 90, 80 sec.

The above data are simply samples, but they show that tran-

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spiring power may be studied and compared for a wide range of physiological types, by the method of cobalt chloride paper as thus far developed. It must be remembered that the transpiring power of plant surfaces varies greatly, not only with the species, but also (for the same species or variety) with the conditions under which the plants have grown, with the conditions immediately preceding the test, with the time of day, and probably with other conditions.

SUMMARY

The foregoing pages have presented improvements that render field tests of plant transpiring power much less arduous and considerably more precise than has hitherto been the case. The elimination of repeated field tests over the standard evaporating surface, and the substitution therefor of a thermometer reading and a simple arithmetical calculation, greatly increase the ease with which determinations may be carried out upon plants in the open. The introduction of composite paper slips, including the two permanent color-standards, makes for much greater precision than has been possible heretofore, and the use of small desiccators for keeping the slips dry and approximately at air temperature, until a test is to be made, add greatly to the ease of field manipulations. Improvements in the standard evaporating surface—now relegated to laboratory use—make this apparatus much less susceptible of accidental alteration, and render its use less troublesome, than has been the case in the past. Finally, the new cobalt-chloride paper is decidedly more uniform than any we have previously used, which is a very important consideration in the application of this method.

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A SUMMARY OF BOG THEORIES[1]

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Various theories have been offered in explanation of the fact that plants other than bog xerophytes are largely inhibited from sphagnum bogs. In this paper the writer has arranged systematically the various theories on this question that have come to his attention and has cited the literature bearing on each so far as he has had access to it.

DEFINITION

By the term "sphagnum bog" the writer means that stage in the physiographic succession of an area during which its surface is entirely devoid of ordinary "hard" soil, and is composed completely of living sphagnum moss under which is fibrous brown peat composed mainly or entirely of partially decayed sphagnum.

This is the sense in which the writer has used the terms "bog" (41, p. 314) and "sphagnum bog" (42, p. 167) with reference to the Puget Sound region and the coastal region of Alaska. It corresponds closely to the following terms of other writers, "sphagnum moor," Sitensky (51) and Warming (60); "sphagnetum" ("raised bog association," "hochmoor"), Ganong (25, p. 442); "hochmoor," Früh und Schröter (23, p. 129); "Cassandra zone," Weld (62, p. 43); "sphagnum-heath zone," Transeau (56, p. 370); "zone of bog shrubs," Burns (1, p. 106); "Bog-meadow association" and "bog heath association," Dachnowski (22, pp. 31–34 and 20, pp. 238 and 244).

A tabulation of the distinguishing characters of the "flachmoor" and of the "hochmoor" has been made by Früh und Schroe-

[1] Paper read at a meeting of the Ecological Society of America at San Diego, California, August 10, 1916.

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ter (23, p. 129). They give the terms "sphagnum moor" and "raised bog" among the twenty-two synonyms for "hochmoor." They also give a comprehensive summary of the literature dealing with the term "moor." Of all of the definitions that had been offered, they could find only four worthy of consideration. All of the four contain as their essential part the idea that the substratum is composed of the products of the decay of plants. The following is a translation of the definition that they accept. It is quoted by them from Weber (61). The parentheses are inserted by Früh und Schröter.

"Moors are (in the main quarternary, mostly alluvial) formations of the surface of the earth which have been formed by plants and which always have at the surface a mass of decomposition products rich in carbon (acid) which consists of pure plant substance (mostly cellulose)."

This definition includes both the "flachmoor" and the "hochmoor." There seems to be nothing in the definition of "sphagnum bog" ("hochmoor") suggested at the beginning of this paper that is inconsistent with it. The parentheses, it will be noted, emphasize three ideas, (a) that these moors occur on either pleistocene drift or on deposits of some sort that have been laid down in post pleistocene times, (b) that the soil water has an acid reaction, (c) that the decay *at the surface* has not gone far enough to break up the cellulose of the sphagnum or other plants involved. The first of these ideas holds generally for the bogs of the Puget Sound region that the writer has seen, for they are mostly on glacial till, but does not seem to hold for all of the bogs of Alaska. The second idea holds for all of the bogs from which the writer has examined water. The third idea seems to be true of all bogs examined by the writer in the Puget Sound region and in Alaska.

Along the borders of sphagnum bogs especially where they overlie glacial till there is frequently a zone of mucky soil on which there is a more or less gradual transition to a less specialized flora. (Cf. Burns 1, p. 120 and Shaw 48, pp. 447–450.) Sphagnum bogs may occur as openings in dense woods (*e.g.*, King County, Washington) or they may occur in treeless regions

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(*e.g.*, southwestern Alaska). They may border on an open lake (*e.g.*, Mud Lake and Echo Lake, King County, Washington) or they may even completely surround the lake (*e.g.*, Little Crystal Lake, Snohomish County, Washington). They may occur in valleys (*e.g.*, Henry bog near Seattle) or in depressions in the tops of considerable elevations (*e.g.*, Monroe, Washington, and Mitrofania Bay, Alaska). They may also occur as relatively small patches in the tundra (*e.g.*, Yakutat, Alaska). As the writer has stated before (42, p. 180) the two conditions that seem to attend the formation of a sphagnum bog are a considerable growth of sphagnum and the accumulation of the products of its slow decay in the absence of drainage.

THE XEROPHILY OF BOG PLANTS

The flora of sphagnum bogs is widely recognized as being prevailingly xerophytic. It is distinctly so in the bogs of the Puget Sound region and of the coastal region of Alaska (Rigg 41, p. 314, 42, p. 181). That is, the plants characteristic of these bogs show such structural characters as we would expect in plants growing in dry places, in spite of the fact that the substratum in which they grow is wet. This is "physiological drought" as distinguished from physical drought.

The view that bogs are not exclusively xerophytic has been advanced by Clements (7, pp. 168–170) and by Burns (1, pp. 105 and 124). It is evident that this apparent difference in opinion is a mere question of the definition of terms. Clements evidently uses the term "bog" in a very broad sense to include swamps and ponds and not at all in the strict sense of "sphagnum bogs." He pictures (p. 169) *Sagittaria latifolia* as a "bog plant." When Burns (1, p. 124) states that "The bogs around Ann Arbor (Michigan) are not xerophytic habitats, as such, but contain xerophytic, hydrophytic, and even mesophytic areas," and that indications are "that xerophytic conditions in bogs of southern Michigan will shortly disappear," he is using the word "bog" to include seven different successional zones the fourth one of which (bog shrubs) is equivalent to the term "sphagnum bog"

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as defined at the beginning of this paper. Burns (1, p. 105) quotes Transeau (55), Livingston (33) Dachnowski (15, 16) and Pennington (38) as supporting his view, but the same facts with regard to definition of terms must be taken into account. Dachnowski (19, p. 513) speaks of the "xeromorphy" of bog plants.

The xerophytic characters of the Ericaceae, which include many of the plants most characteristic of the sphagnum bogs of the Puget Sound region and of the coastal region of Alaska (e.g. *Ledum*, *Kalmia*, *Loiseleuria*, and *Andromeda*), have been described by Solereder (54), H. E. Peterson (39), O. G. Peterson (40), Boergesen (4) and Breifeld (6). The ecological anatomy of bog plants has been described by Transeau (58, pp. 17–20). Lists of plants characteristic of bogs have been given by Cowles (9, pp. 35–37), Transeau (55, p. 403), Burns (1, p. 106), Dachnowski (15, p. 131; 22, pp. 33–34 and 20, pp. 238–248), Nichols (35, p. 204), Pennington (37, p. 56); Rigg (41, p. 314 and 42, p. 181) and others.

WHY ARE PLANTS CHARACTERISTIC OF SPHAGNUM BOGS MAINLY XEROPHYTIC?

a. They may be glacial relicts. More or less support for this theory has been found (Dachnowski 18, p. 1) in the general opinions given by Gray (26) and by Hooker (28). So far as the writer has been able to find, however, neither of these botanists made any direct statement with regard to the theory that bog plants are glacial relicts. They emphasize the general idea that arctic plants came south as a result of the advance of the ice sheet. Some support for this theory is found in the writings of Dachnowski (18, p. 1), Harshberger (29), Transeau (55, pp. 409–420) and Schwendener (50). Nichols (35, pp. 212–216) discusses this view but endorses it only with qualifications. He quotes (p. 216) a letter from Dr. Charles A. Davis stating that the theory of glacial influence except so far as the ice sheet provided favorable topographic conditions for the growth of bogs is practically untenable. Clements (p. 170) states: "The presence in bog plants of modifications characteristic of xero-

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phytes seems to be explained . . . . by their ability to adjust themselves to changed conditions without undergoing a corresponding change in structure . . . . The . . . . (xerophytic features found in some amphibious plants) were developed when these species were growing in zerophytic situations."

b. They may be relicts from a former more general distribution of boreal plants under different climatic conditions than we now have. This opinion has been expressed by Dr. H. C. Cowles in his lectures. This view is also taken by Nichols (35, pp. 215–216). Compare also Transeau (55, pp. 409–420).

c. They may have been rendered xerophytic by bog conditions. This view has been endorsed by Whitford (63, pp. 314–315). Nichols (35, p. 212) says " . . . . soil conditions satisfactorily account for the phenomonen of bog xerophytism . . . ." Nilsson (without citation, possibly 35) is quoted by Burns (1, p. 122) as attributing differences in structure between swamp and bog plants to a difference in the food supply. It has been shown by Transeau (57, p. 867) that bog conditions do to a certain extent induce xerophytism. It has also been observed by the writer that *Ledum* and *Kalmia* grow much more vigorously and show less of xerophytic appearance of their leaves when growing outside of bogs than when growing in them.

All of these theories must be considered in attempting to account for the xerophily of the plants of sphagnum bogs. So far as glaciated regions are concerned (a) seems to have much weight, but when we remember that sphagnum bogs are not confined to glaciated regions it is evident that careful consideration must be given to (b). The facts mentioned in (c) must also be considered.

HOW ARE PLANTS OTHER THAN BOG XEROPHYTES INHIBITED FROM SPHAGNUM BOGS?

To the mind of the writer this question has much more interest than the question just discussed. The following suggestions have been made in regard to it.

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a. "Physiological dryness," because of abundant soluble salts and humous acids. This is suggested by Schimper (52, pp. 4, 8, and 658). It is approved by Dachnowski (18, p. 148). The term "physiological dryness" is too indefinite to express any exact factor. In so far as it might mean any chemical effect of the acids or salts it is discussed in (*b*) and (*c*). In so far as it might mean high osmotic pressure of the surrounding medium, it is discussed in (*e*).

b. Humous acids. This has received some support from Schimper (52, p. 8) and from Warming (60). The writer knows of no experimental evidence tending to establish this as a factor. It must be considered in the light of the statement by Schreiner (49, p. 579) that "humic acid" has absolutely no existence and that the substance so called is a mixture of widely differing compounds and in the light of the suggestion by Wieler (64) that "humic acids" in soils are inorganic acids resulting, for example, from the decomposition of salts. Skene (46) finds that the sphagnums thrive best in acid solutions, since mineral solutions, although generally physiologically harmless, may be ecologically harmful.

c. Soluble salts (*e.g.*, Humus salts). This is also suggested by Schimper (p. 658). So far as the writer has found this is a mere suggestion, made without the evidence of any experimental data. According to Schreiner (49, p. 579) the term "humates" would also lose its meaning.

d. Acidity as such (H ions). Negative experimental results on this have been obtained by Livingston (33, p. 355) and a negative view of it has also been taken by Dachnowski (15, p. 132 and 16, p. 404).

e. High osmotic pressure of the water in the substratum. Whitford (63, p. 314) suggested that this might be a factor. Negative results on this have been obtained by Livingston (32, p. 385), and Rigg, Trumbull, and Lincoln (44), Transeau (58, p. 37) and Dachnowski (15, p. 132 and 19, p. 505 and 510) have also rejected this as being a factor of any considerable importance. Dachnowski (16, p. 390) states: "During the changes which the accumulated plant material undergoes in

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the process of peat making there are alterations and reductions leading to gaseous and colloidal products but little known." The writer (43) has found that there is a considerable amount of colloidal matter in filtered bog water.

The thesis that in general, the relations between plants and the soil are chiefly determined by the concentration of the soil solution and the limits within which it may vary has been defended by Gola (12) and (27). He contrasts the colloidal and the crystalloidal characters of the soil.

f. Low temperature of the substratum. This was suggested by Kihlman (31) and has received support from Früh and Schroeter (23), Transeau (57, p. 867 and 56, p. 358–360), and Cox (11, p. 222), and is discussed by Burns (1, p. 110). It has been rejected by Transeau (58, p. 364) as being inadequate to account for conditions in the bogs of southern Michigan. Dachnowski (18, pp. 138–139) does not believe that the topographical distribution of plants in bogs can be accounted for on the basis of low temperatures of the substratum. Transeau (58, p. 36) has noted that low temperatures may retard chemical action, diffusion and osmosis and keep down bacterial action. The evidence from Cox's work (10, pp. 45, 82, 119) is that low soil temperature is an important factor.

g. Low temperature of the air over the bog. The observations of Burns (1, pp. 108 and 110) and of Cox (10, pp. 46, 81) indicate that this is a factor.

h. Difference between air temperature and soil temperature. Dachnowski (18, p. 139) decides that this is not a factor of sufficient importance to enter into the problem. It was suggested by Transeau (55, p. 419). Cox's data (10, pp. 69, 78, 82) seem to indicate that it is an important factor.

i. High evaporating power of the atmosphere (*e.g.*, drying winds). This has been suggested by Kihlman (31) as acting in connection with (*f*). Dachnowski's (18, pp. 143–144) experimental evidence is unfavorable to this view. Cox's data (10, pp. 98–109) are also unfavorable to it. The situation of many of the bogs in the Puget Sound region makes it evident that this is probably not an important factor in them.

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j. Lack of aeration of the substratum. This factor has the approval of Transeau (58, p. 38), Früh and Schroeter (23), and Whitford (63, p. 314). Dachnowski (15, p. 141) states: " . . . . results reported as due to lack of aeration in the bog substratum are really due to toxicity." Transeau (58, p. 39) finds that lack of aeration favors the growth of mycorrhiza on roots of *Larix*. This may suggest a question as to whether the growth of mycorrhiza in bogs inhibits mesophytes or at least gives advantage to xerophytes. Nabokisch (34) believes that intramolecular respiration in low oxygen pressure gives rise to products that are toxic when concentrated, though stimulatory when dilute. It seems probable to the writer that lack of aeration is a factor, at least indirectly.

k. Abundance of methane. It is of course well known that methane is formed by decay with deficient supply of oxygen. An inflammable gas has been obtained by thrusting a piece of gas pipe or in some cases even a pole into bogs in the Puget Sound region. The writer has seen no evidence as to how much influence this factor may have. It should be considered in connection with (*j*).

l. Deficiency in "available" nitrogen. Transeau (58, p. 37) makes the statement that "Bog soils are notable deficient in . . . . available nitrogen." Jodidi (30) found no nitrates in the Michigan peat soils examined. He found that practically all of the nitrogen was of organic nature and that the amount of water-soluble nitrogen increased slowly with weathering. He says that the amount of ammonia ("representing the nitrogen immediately available as plant food") is sufficient in brown peat to provide for one or two crops under cultivation. He found monamino acids, amides and diamino acids.

Robinson (45) found that 25 per cent of the nitrogen of peat is converted by hydrolysis into primary amines, probable forming amino acids, and that 10% is present as acid amides. He says that the greater part of the nitrogen in peat occurs in numerous unknown forms, "which may represent the most important factors in aiding or inhibiting plant growth." He expresses the belief that the greatest need at present in determining the

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value of the organic nitrogenous matters in peat is a clear knowledge of the individual substances actually present in such material.

Schreiner and Shorey (47, p. 43) have isolated organic compounds from peat soils and have emphasized the fact that a vast number of chemical compounds are added to the soil on the death and decay of plants. Skene (46) found that the "Sphagna do actually utilize in growth the bases held absorbed by the acid compounds of the cell walls."

Dachnowski (17, p. 332) believes that nitrogen in peat is bound up in organic compounds unavailable for growing cultivated plants. He reports (18, p. 11) that the relative availability of peat nitrogen is 8 per cent to 12 per cent, but that this can be greatly increased by composting with the bacterial life from stable manure. He suggests (19, p. 514) that organic nitrogenous products of the activity of micro-organisms may be absorbed and assimilated by some plants. He states (21, p. 62) that "Every green plant is undoubtedly able to a certain extent to assimitate nitrogenous and other organic compounds."

Coville (13, pp. 44–48) found that peaty soils are deficient in "available" nitrogen because nitrifying bacteria cannot thrive in these soils on account of their acidity. He sees indications that the mycorrhizal fungus of the swamp blueberry transforms "nonavailable" nitrogen to "available" nitrogen and possibly even transforms free nitrogen of the air into a form suited for the use of the blueberry plant. It seems equally possible that this might be true of other bog plants.

Coville (8, p. 6) also states that "It is conceivable that a crop plant might utilize nitrogen that existed in organic form in soils." If we distinguish between "available" and unavailable" nitrogen it may be possible that plants not having mycorrhiza and not capable of using insect food may be at a disadvantage in sphagnum bogs because of a deficiency in "available" nitrogen. Bottomly (5, p. 539) finds evidence in his experimental work on bacterized peat for suggesting that plants depend not only upon the supply of mineral food constituents but also upon a supply of certain accessory organic food substances, very small

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amounts of which are sufficient to supply the needs of the plant. He found that bacterized peat after sterilization was an excellent medium in which to grow nitrogen-fixing bacteria and apply them to the soil. Schreiner (49, p. 583) has formulated the theory that "degradation products of proteins are absorbed directly by the plant from the soil and that the plant uses these units for building up the complex proteins as far as it is possible to do so." Skinner and Beattie (53, pp. 432 and 437) have shown that wheat plants can utilize asparagin from soils. They also quote other workers who have shown that asparagin is beneficial to maize, oats, barley, radishes, and *Lemna* in water cultures. It would thus seem that it is difficult to draw a hard and fast line between "available" and "unavailable" nitrogen.

m. The activities of micro-organisms. Dachnowski (17, p. 333) finds reason for believing that bacteria are agents in enabling sphagnum bogs to admit certain plants and exclude others.

n. Water-holding power of peat. Burns (1, p. 123) suggests this and also quotes Davis (14) as favoring this view. Coville (13, p. 38) gives the following figures for the moisture equivalent of the soils mentioned—Kalmia peat 142%, clay 30%, loam 18%, sand 2% to 4%.

o. The depth of the water table in summer. Burns (1, p. 116) finds reason for believing that this is a factor and quotes Davis (14) in support of this view. Dachnowski (20, p. 241) states that "Variations in the position of the water table do not influence the (Oxycoccus-Sphagnum) association so greatly as is often stated, nor do they offer an explanation of the xerophytic structure of the plants." The water table certainly goes very low in late summer in many Puget Sound bogs but water can be readily squeezed from handfuls of sphagnum obtained only a few centimeters beneath the surface. (But cf. Burns, 1 p. 116, and Coville 13, pp. 38 and 39.)

p. Low surface tension of water. Blackman (3) reviewing the work of Czapek and Lepeskin suggested that low surface tension of the surrounding medium might cause the loss of water from plant cells and thus work directly against osmosis and that this might destroy the efficiency of the growing points of roots.

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He does not suggest this with reference to bogs but the idea seemed to the writer to be worth consideration in that connection. Rigg, Trumbull, and Lincoln (44) found no evidence for considering this a factor since the surface tension of all bog waters tested was much greater than the value (0.68 of that of distilled water) which Czapek determined to be the surface tension of plant protoplasts.

q. Toxic substances in the substratum. This was suggested by Livingston (32, p. 385; 33, pp. 354–355) and experimental evidence to support it has been furnished by Dachnowski (15, p. 141; 16, p. 403; 17, p. 339; 20, p. 318) and by the writer (41, p. 318). Transeau (58, p. 38) finds that " . . . . local (Michigan) bog water has no tendency toward the production of xerophilous modifications." The large amount of varied experimental evidence on this theory leads the writer to regard toxicity of the water as a very large factor in the inhibition from bogs of plants other than bog xerophytes. The writer has found experimental evidence (43) tending to indicate that colloidal matter in the water is a large factor in its toxicity.

r. Bog plants are more plastic than other plants (Dachnowski 19, p. 513).

s. Bog plants in contact with peat soil may cause the injurious organic compounds to be precipitated in insoluble form while other plants do not have this effect (Dachnowski 19, p. 514).

WHAT ARE THE POSSIBLE SOURCES OF THE TOXIC SUBSTANCE OR SUBSTANCES IN BOG WATER?

a. Excretion products of subterranean portions of higher plants. Dachnowski (15, p. 141 and 16, p. 403) has suggested this.

b. Products of the metabolism of bacteria, fungi and protozoans. Dachnowski's (19, p. 513) work on bacteria in bogs suggests this.

c. The decay of sphagnum moss. The writer (41, p. 324) has called attention to the fact that since the presence of sphagnum moss and the lack of drainage are the two conditions neces-

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sary for the formation of bogs it seems probable that in this combination would be a good place to seek for the production of the toxic substance or substances. Bauman and Gully (2) have found that the acidity of peat soils is due to the fact that the colloidal matter of the cell covering of the hyaline sphagnum cells retains chiefly the basic ions of the dissolved salts contained in the cells, the acid ions being thus freed and rendering the soil water acid. It is not established, however, that acidity is the cause of the toxicity.

d. The decay of plants other than Sphagnum. This in connection with (*c*) has been suggested by Dachnowski (15, p. 140 and 19, p. 514).

e. The absence of any adsorbing agent such as ordinary soil. This was suggested by the writer (41) since the toxicity of bog water can be removed by means of adsorbing agents (Dachnowski 15, p. 134; 16, pp. 397 and 407). The effect of adsorbing agents on toxins was established by True (59, p. 15).

HOW DO THE TOXIC SUBSTANCES IN BOG WATER ACT ON PLANTS?

a. By causing a change of form of the plant. Livingston (33, p. 351) found this to be true of *Stigeoclonium*.

b. By causing xerophytic structures. Transeau (57, p. 867) found this to be true of *Rumex acetosella*.

c. By decreasing growth. Dachnowski (15, pp. 132–141 and 20, p. 311) found this true in his experiments on the growth of agricultural plants and *Marchantia* gemmae in bog water.

d. By decreasing absorption. This was suggested by Schimper (52, p. 4).

e. By decreasing transpiration. Dachnowski (15, p. 140).

f. By decreasing absorbing surface. This seems to be established, at least in some cases, by the work of the writer (41, p. 318). Dachnowski (18, p. 15) disagrees with this view. Coville finds that the roots of *Vaccinium corymbosum* whose favorite habitat is peat are entirely devoid of root hairs.

g. By increasing absorption to such an extent that it interferes with the efficiency of root tips as growing organs.

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h. By changing the permeability of the protoplasts. This has been suggested by Dachnowski (19, pp. 513, 514, and 21, p. 62) and is in accord with the current conception of the way in which toxins act on plants.

Although much of the literature cited in this paper deals also with the physiographic history of bogs, no attempt has been made to review the literature of that phase of the subject. The writer has chosen to confine his attention in this paper to an effort to systematize the matter relating to the xerophily of the plants characteristic of the particular physiographic phase for which he has suggested a definition at the beginning of this paper and to the large inhibition of mesophytes from this phase.

The literature listed at the end of this paper includes only the papers to which citations have been made. While care has been taken as to the accuracy of the citations and no effort has been spared to make them complete, it is scarcely to be hoped that the list is free from errors or omissions.

The writer acknowledges with pleasure his indebtedness to Prof. H. C. Cowles for several conferences on bog problems, and to Prof. William Crocker for suggestions in regard to the literature on toxicity.

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BOOKS AND CURRENT LITERATURE

How to Know the Mosses.—Mrs. Dunham's book, How to Know the Mosses[1] aims "to present mosses in a simple, non-technical way, so that the student may recognize at least their genera and in some cases their species without depending upon the use of a lens." This book is in some respects unique and in the mind of the reviewer it represents about as nearly the ideal as can be hoped for in dealing with a fairly difficult group of small plants.

The book has resulted from the work of several years in trying to get usable keys not requiring a lens, and the author has not hesitated to enlist the services of friends and co-workers in the preparation and testing of such keys. It contains 287 pages, is attractively printed, and is well illustrated by six full-page plates and 115 text figures, the illustrations being line-drawings by the author, mostly in natural size. The book contains the following headings: Abbreviations of Names of Authors; Introduction, Habit and Manner of Growth, Leaves, Capsules, The Keys Explained, How To Use the Keys; Helpful Suggestions, Key to Distinguish Mosses from Common Hepatics and Lichens, Leaf Key to Genera, Capsule Key to Genera, List of Genera. Then comes the descriptive part of the work (pages 73–257), and the book ends with Helps to Identification of the Most Common and Conspicuous Mosses, Glossary, and Index.

In using the key one first traces the plant through the leaf key by characters such as habitat, length of stem, shape of leaves, etc., this leading to one or more numbers referring to genera treated in the text, to which one turns for further distinctions or verifications. By using the capsule key, constructed similarly to the leaf key, another series of reference numbers is obtained and, by elimination of the numbers not obtained by the use of both leaf key and capsule key, the list of genera to be referred to in the text is often considerably reduced, or even narrowed to one. The keys are uniform in treatment and easy to work.

[1] Dunham, Elizabeth Marie, How to Know the Mosses. Houghton, Mifflin Company, Boston and New York, 1916 ($1.25).

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To readers of THE PLANT WORLD this book will be of particular interest in that the habitat is particularly emphasized as of value in classification. In the keys to the genera the eighteen main headings, set up in black-face type, are subdivisions according to habitat, *e.g.*, Plants growing on the ground, Plants growing on roots or trunks of trees, etc., thus practically classifying the mosses on an ecological basis. Many workers in ecological plant geography have been too prone to only roughly classify, or to leave out altogether from their ecological lists, the names of the smaller mosses: and to such workers we would particularly recommend Mrs. Dunham's book.

This book will be of value not only to the amateur bryologist and to the ecologist who does not pretend to be a bryologist, but even to the professed bryologist who knows the species as they appear under the microscope. It is essentially a *field-book*, and the emphasizing by italics of the most prominent naked-eye characters seems, at least to the reviewer, to constitute a most valuable contribution to our bryological literature. The present writer has tested the book on several occasions, both in Pennsylvania and in northwestern Ontario, and the results have been quite satisfactory.

The book takes up, altogether, 80 genera and about 150 species, the author remarking that: "The mosses included in the Keys are those that are commonly or occasionally collected in the northeastern part of the United States. But the Keys really cover a much larger field, many of the mosses being widely distributed, as will be seen by reading the range given with each genus or species." With regard to the relative abundance of the various species described, the book would seem to apply more particularly to the New England States, and due allowance should be made for this by those using the book farther to the south or southwest. The species treated in the book comprise probably from one-third to one-half of those in the moss-flora of most localities in the eastern two-thirds of the United States, but in point of relative abundance and of conspicuousness the proportion treated would appear considerably larger.

As would naturally be expected, little or no attempt has been made by Mrs. Dunham to separate the species of genera which embrace minute plants or whose species are separable only by microscopic characters. Among the genera in which little or no attempt has been made to separate the species, the following may be noted: *Sphagnum*, *Andreaea*, *Fissidens*, *Orthotricum*, *Pylaisia*, *Leskea*, and *Thuidium*.

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The nomenclature followed by Mrs. Dunham is that of Brotherus in *Die Natürlichen Pflanzenfamilien.* Synonyms are given wherever deemed desirable and the generic names have been divided into syllables and accented to show their pronunciation according to the customary English method of pronouncing Latin.

The reviewer would recommend this book particularly to all who are interested in knowing something of mosses in the field, whether amateur or more technical bryologists, and it is believed and hoped that the book will interest large numbers of people in the mosses because of its suitability both for the amateur and for high-school and college students who, in their school work, would have but little time to devote to learning to recognize the species.—O. E. JENNINGS.

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NOTES AND COMMENT

It is often difficult, under existing conditions, for a young man who is seeking a position in botany, or any of the allied sciences, to bring his qualifications to the attention of those who might wish to secure his services. Those upon whom it devolves to fill the vacant posts and chairs in our profession, or to secure men for new developments, often experience an equal difficulty in learning who are the eligibles from whom they might select. With a view to aiding both sides of this situation THE PLANT WORLD has inaugurated a Professional Advancement Column, which will be maintained continuously in its advertising pages provided it is given any support whatever. This column is designed primarily to serve the men who are seeking professional positions, but it may also be of utility to those who are desirous of advertising for men of particular qualifications. Further details of the plan will be found in the advertising pages of the present issue.

The sixth volume of the Memoirs of the New York Botanical Garden is devoted to the publication of some thirty-six papers which were presented at the Twentieth Anniversary of the Garden in September, 1915. The following titles will serve to indicate the scope of the contents: The mechanism and conditions of growth, by D. T. MacDougal; Observations on inheritance of sex-ratios in *Mercurialis annua*, by Cecil Yampolsky; Triassic plants from Sonora, Mexico, by Edwin W. Humphreys; A white cedar swamp at Merrick, Long Island, and its significance, by Norman Taylor; On the nature of types in Pediastrum, by R. A. Harper; Endemism as a criterion of antiquity among plants, by Edmund W. Sinnott; The development of *Lepiota*, by George F. Atkinson; Plant ecology and the new soil fertility, by Charles B. Lipman; Self- and cross-pollinations in *Cichorium intybus* with reference to sterility, by A. B. Stout; Vegetative life zones of the Rocky Mountain region, by P. A. Rydberg; The embryo-sac and pollen grain as colloidal systems, by Francis E. Lloyd; The vegetation of Anegada, by N. L. Britton.

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The chair of tropical forestry recently established in the Yale Forest School has been filled by the appointment of Dr. H. N. Whitford, who is well known for his investigations in the Philippine Islands, and has been more recently engaged in work for the Canadian Commission of Conservation in British Columbia. During the present year Dr. Whitford is offering a general course of lectures on tropical forestry and a course on wood structure. The practical work in connection with these courses will be carried on in South America.

The University of Vermont has published a new bulletin entitled The Trees of Vermont, prepared by Professor George P. Burns and Professor C. H. Otis. The usual keys, descriptions and notes regarding habitat and distribution are given for the native trees, and a series of drawings and descriptions make possible the identification of the wood of some of the commonest species.

The Department of the Interior has issued a portfolio of booklets describing nine of the leading National Parks of the United States. The numerous and excellent illustrations give the portfolio a substantial value to everyone who is interested in the larger aspects of nature.

Professor Frank L. Stevens has published a monograph of the Porto Rican species of *Meliola*, a tropical genus of ascomycetous fungi parasitic on the leaves of a wide range of higher plants (Illinois Biological Monographs, II, 4).

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SELECTIVE PERMEABILITY AND THE PLASMA-MEMBRANE

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A necessary condition for plant nutrition and, consequently, for plant growth is that substances from the outside must enter the plant. Some of these substances come from the atmosphere and some from the soil through the medium of the soil solution. The substances which come from the atmosphere enter the plant by simple diffusion. The case, however, is not so definite and clear with reference to those substances which come from the soil. It is not definitely known whether they enter by diffusion or whether there are other forces involved—physical, chemical, or forces which lie beyond our present knowledge which are generally designated as vital.

The diffusion alternative would simplify matters very much. The limited number of mineral elements found in plants could be accounted for in three ways:

1. The elements found in plants are those which make up principally the soil solution.

2. The metabolic processes of the cell may exert a regulatory function with reference to the intake of the mineral elements; those which are found in plants enter in chemical combinations with the organic products of metabolism and are thus accumulated, while the others, if they do enter the plant, are present in too insignificant quantities to be detected by chemical analysis.

3. Only those elements which are found in plants can enter the plant cells, because of selective diffusion.

The diffusion possibility, however, is not borne out by facts obtained in experiments concerned with measurement of the permeability of plant cells to different substances. When, for instance, seedlings are grown in a balanced solution of electro-

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lytes, as calcium nitrate, potassium sulphate, etc., their mineral content increases with their growth. The electrolytes of the nutrient solution must, consequently, enter the plant cell. We know further that sugars are translocated in plants and that heterotrophic plants can absorb sugar directly from a sugar solution; consequently, sugar must be capable of entering and leaving the plant cell. But when the permeability of plant or animal cells is measured by the plasmolytic method it is found that such cells are permeable neither to electrolytes, nor to sugar, for the plasmolysed cells never regain their original form so long as they remain in hypertonic solutions of these substances.

Using the same plasmolytic method it is found that there are in addition to the substances which produce irreversible plasmolysis, many substances (monohydric alcohols, aldehydes, peptones, etc.) which do not produce plasmolysis at all, and, consequently, enter the cell very easily; and that there are numerous substances (dihydric alcohols, glycerine, the amids of the monobasic acids, etc.) which produce reversible plasmolysis, the plasmolysed cells recovering while in the hypertonic solution with varying rapidity and, consequently, enter the cell slowly.[1]

The explanation of the plasmolytic phenomena is based on the difference in osmotic pressure within and outside of the cell and on the property of selective permeability. When a living cell is placed in a hypertonic solution the osmotic pressure in the surrounding medium is greater than within the cell, and, as a result, water is drawn from the cell and plasmolysis takes place. When the cell is impermeable to the substance in solution the plasmolysis is irreversible as long as the cell remains in the hypertonic solution. When, however, the cell is permeable to the solute equal concentration and, consequently, equal osmotic pressure are eventually obtained within and without the cell through diffusion and the cell assumes its previous form, *i.e.*, the plasmolysis is reversed.

Unless the interpretation of the plasmolytic phenomena is

[1] Overton, E., Über die Allgemeine Osmotischen Eigenschaften der Zelle. Vierteljahrschrift. Naturf. Ges. in Zurich **44**: 88–135. 1899.

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not true, or unless there are some other factors involved which cause plasmolysis or prevent its reversibility in case of electrolytes and sugars, we are confronted with the fact that the cell is impermeable to substances of the highest importance in plant nutrition, while it is permeable to substances which are non-essential or are of no value at all. It is possible that the impermeability of the cell to the essential food elements is a provision on the part of the cell against exosmosis while it is provided with some means unknown to us for absorbing these elements and translocating them from cell to cell.

As it is, the plasmolytic phenomena are considered as one of the means to demonstrate the property of selective permeability of living cells. It is further demonstrated by the behavior of the living cell toward aniline dyes which was first studied by Pfeffer.[2] In this case the permeability can be studied more directly as the entrance of the dye is observed by the coloring of the cell sap. It is, however, possible that observations of this kind refer only to the accumulation of the dyes.[3] The property of selective permeability of the cell is further shown by the facts that colored cell sap never enters the surrounding living protoplasm and that cherries and red beets color water only after the cells have been killed by heating.[4]

The question arises where is the seat of this property of selective permeability. Is it the entire mass of cytoplasm or only its limiting surfaces. This brings up the question of the existence of special plasma-membranes, *i.e.*, whether the limiting layers are of a different chemical or physical nature than the rest of the cytoplasm or not.

Physiologists are inclined to answer the question in the affirmative. Pfeffer[5] distinguishes between the "ectoplasmic" membranes which separate the cytoplasm from the cell wall and the endosplasmic membranes which are in immediate contact with

[2] Pfeffer, W., Über Aufnahme von Anilinfarben in lebenden Zellen. Unter. a. d. Bot. Inst. Tübingen **2**: 179–332. 1886.

[3] Ruhland, W., Beiträge zur Kenntnis der Permeabilität der Plasmahaut. Jahrb. Wiss. Bot. **46**: 29. 1908.

[4] Höber R., Physik. Chemie der Zelle und der Gewebe, 53. 1906.

[5] Pfeffer, W., Pflanzenphysiologie, 86–94. 1897.

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the vacuole. It is these membranes which are, according to him, responsible for the osmotic properties of the cell and for its selective permeability. He does not agree with DeVries that the plasma-membranes originate from specific tissue, but thinks that any part of the cytoplasm may be transformed into a membrane when exposed to the surrounding medium, as it is shown by the formation of vacuoles in the protoplasm which is pressed out from a young root hair of *Hydrocharis morsus-ranae* when it comes in contact with colored water. It is the contact with the surrounding medium and the cell sap, which, according to Pfeffer, causes the respective membranes to be formed. He is inclined to think that the molecular forces involved in the phenomenon of surface tension play an important rôle in the formation of the plasma-membranes, but he does not think that they are the only cause. The contact with the surrounding medium may precipitate substances in the peripheral film of protoplasm thus transforming it into a plasma-membrane. He believes that the nature of the surrounding medium exerts some influence upon the formation of the plasma-membrane, but the nature of that influence and the extent to which it modifies the osmotic properties of the cell are not as yet known. The properties acquired by the plasma-membrane are not permanent, according to Pfeffer, and it is transformed into ordinary protoplasm when it happens to be removed from the periphery into the inner layers. It is evident that, according to Pfeffer's conception, the differences between the plasma-membranes and the rest of the cytoplasm are rather of a physical than of a chemical nature.

The following evidence is offered in favor of the existence of special plasma-membranes.

(1) When cells of a root hair of *Hydrocharis* are placed in an isotonic solution of cane sugar to which a trace of hydrochloric acid is added, the protoplasm becomes turbid, its streaming stops—it is evidently killed. When the solution is then colored with eosin the coloring matter does not enter the cells, notwithstanding the fact that the protoplasm in them is dead. When, however, the cells are transferred into a colored hypotonic

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solution, it is observed that the dye begins to penetrate the cell from certain points on its surface and that it is then distributed gradually all over the protoplasm. The explanation is that the protoplasm which is permeable to the dye can not be stained till the plasma-membrane is ruptured by the influx of water.

The question is, asks Höber, why a healthy cell does not behave in the same way when introduced in a colored hypotonic solution?[6]

(2) When a thread of *Spirogyra nitida* is placed in a 10% solution of potassium nitrate colored with eosin, the vacuoles resist for a time the entrance of the dye after the entire plasmolysed contents of the cells are killed and stained. This would tend to indicate the existence of a vacuolar plasma-membrane as the protoplasm in immediate contact with the vacuole seems to behave differently from the entire cell content.[7]

(3) Lepeshkin[8] has observed that when a thread of *Spirogyra* is pressed under the microscope by the cover glass, the external layer of protoplasm seems to die, while the remaining mass of protoplasm falls apart into balls some of which contain considerable quantities of cell sap. The explanation is that the entire mass of protoplasm was held together by the plasma-membrane and fell apart when it was killed.

The evidence, as it is seen, is too indirect and inconclusive. The facts reported could be explained in a variety of ways besides the existence of special plasma-membranes. Thus, the behavior of the dead cells of the root hair or *Hydrocharis* when transferred from a hypertonic to a hypotonic solution can be explained by the rupture of the entire cytoplasm, as well as by the rupture of the plasma-membrane. The evidence in favor of the existence of vacuolar membranes can be explained by the fact, as it was suggested by McClendon,[9] that the granular protoplasm absorbs the dye and thus prevents it for some time

[6] Höber, l. c., p. 54.

[7] DeVries, Pringsheims Jahrb. **16**: 465. 1885. Höber, l. c. p. 56.

[8] Lepeshkin, W. W., Zur Kenntnis der Plasma-membrane. 1 Ber. d. Deut. Bot. Ges. **28**: 91–105. 1910.

[9] McClendon, J. E., The osmotic and surface tension phenomena, etc., Biol. Bul. **22**: 113–162. 1912.

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from entering the vacuole. The behavior of the *Spirogyra* cells, reported by Lepeshkin, can be explained by mechanical disintegration, similar to the falling apart of a large drop of fluid into a number of smaller droplets.

A special feature of the evidence in favor of the existence of special plasma-membranes is that it all deals with dead or injured cells.

Pfeffer[10] who is firmly convinced of the existence of plasma-membranes admits that the evidence in favor of this theory is as yet insufficient. The question, according to him, would be considered definitely settled, if it were possible to prove that substances distributed in the internal mass of the protoplasm appear neither in the vacuoles nor in the outside medium. Evidence of this kind, however, is wanting. Höber[11] determined the electric conductivity in the interior or erythrocites and having found it to be many times greater than in the erythrocites as a whole concluded that the plasma-membrane was impermeable to ions present in the protoplasm. Kite[12] on the other hand came to the conclusion (on the basis of unpublished data) that the property of selective permeability is possessed by the entire cytoplasm.

Nevertheless the existence of special plasma-membranes is tacitly acknowledged by most physiologists, and many of the hypotheses offered to explain the osmotic and diosmotic properties of the cell are based on this assumption. Pfeffer[13] however and, more recently, Lepeshkin[14] do not necessarily associate the properties of the cell with the existence of plasma-membranes on the inner and outer boundaries of the cytoplasm and admit the possibility that the entire cytoplasm may serve as a thick plasma-membrane. It may be added, that, taking into consideration Pfeffer's conception of the formation of the plasma-membrane, it is hard to conceive how its existence could in any way influence

[10] L. c., p. 91.
[11] Höber, Arch. f. d. Ges. Physiol. **133**: 237. 1910. McClendon l. c., p. 117.
[12] Kite, G. L., The relative permeability, etc. Biol. Bul. **25**: 1–7.
[13] L. c.
[14] L. c.

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the properties of the cell, since according to that conception, the entire cytoplasm is a potential plasma-membrane and, consequently, as soon as one hypothetical membrane is ruptured another one is immediately formed in its place.

Many attempts have been made to account for the selective permeability of the living cell toward dissolved substances. The first explanation that suggested itself was that the plasma-membrane acted as a sieve allowing molecules of smaller size to pass and barring those of larger size, but this hypothesis had to be abandoned inasmuch as by the means of studying permeability which are at our disposal it was found that there is no relation between the size of the molecule and its ability to enter the cell. It was thus found that the plasma-membrane is permeable to the large molecules of alkaloids while it is impermeable to the comparatively small molecules of the amino acids. The case was found to be the same with reference to the artificial ferrocyanide membrane which is, for instance, permeable to sodium salycilate, while it is impermeable to potassium sulphate.[15] The other hypotheses which have been offered in explanation of the diosmotic properties of the cell are based on the solubility in the plasma-membrane. The plasma-membrane, according to this view, represents a continuous layer of a substance which has definite solvent properties. Only those substances which are soluble in the plasma-membrane are capable of entering the cell. The different hypotheses differ with reference to the chemical nature of the substance or substances constituting the plasma-membrane which conditions its solvent properties.

Quinke[16] came to the conclusion, on the basis of his studies of the periodic expansion of fluid surfaces and of the motion phenomena caused by it, that the cell content is enveloped by a thin oil membrane and that thin oil lamella with solid and fluid protein impregnate the entire mass of protoplasm. The alkaline proteins react with the fatty acids contained in the oil; and protein soaps are periodically formed which dissolve and expand on the border between the oil and the surrounding fluid.

[15] Höber, l. c., p. 167.

[16] Quinke, G., Annalen d. Physik und Chemie N. F. **53**: 622. 1894.

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This periodical expansion of the water solution of the soaps, offers, according to him, a physical explanation of the inner movements of the plant cell. The oil membrane, according to him, conditions the diosmotic properties of the cell,—only those substances which are soluble in oil can enter the cell. Quinke offered very little evidence in favor of his hypothesis and it has not met with serious consideration among physiologists.

Overton's lipoid theory, which is very similar to Quinke's, has on the contrary, found very many followers among plant and animal physiologists. His views were evidently formed independently of Quinke as he never refers to him in his works. He carried out extended investigations on the penetrability of a large number of compounds into the living cell and studied at the same time the solubility of these compounds and the nature of their solvents. These parallel observations led him to the conclusion that the plasma-membrane stands in its solvent capacity very near to the fatty oils. On the basis of further consideration, however, and on the basis of the fact that algal threads preserve for a long time their diosmotic properties in a 2% solution of sodium carbonate which would be sufficient to saponify the oils if they were present, he concluded that these are not the substances which condition the selective permeability of the cell.[17] The lipoids, which are non-saponifiable oil-like substances, he found, were analagous in their solvent properties to the plasma-membrane. He found that all dyes that are capable of passing through the plasma-membrane, as may be observed by the coloring of the cell sap, are very soluble in melted cholesterin and in solutions of cholesterin, lecithin, cerebrin and other lipoids. When these lipoids are suspended in a water solution of anilin dyes to which the plasma-membrane is permeable they rapidly absorb the dye. On the basis of these observations and taking into consideration the fact that lecithin and cholesterin are always found in plant and animal cells, he advanced the hypothesis that it is the impregnation of the plasma-membrane with lipoids that accounts for

[17] Ruhland, l.c., pp. 3–4.

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the diosmotic properties of the cell.[18] Since, however, the cell is permeable to water, he abandoned the possibility that cholestrin is the material that constitutes the plasma-membrane (since it is absolutely impermeable to water) and limited the lipoids of the plasma-membrane to compounds of cholesterin, as lecithin, lanolin, etc., which on swelling become permeable to water.[19]

Examining the chemical nature of the dyes experimented upon, Overton[20] found that it is the basic dyes that are soluble in lipoids and are capable of passing through the plasma-membrane, while the sulfonic acid dyes are neither soluble in lipoids nor capable of entering the cell. He explained this phenomenon by the fact that the basic dyes being salts of weak acids undergo hydrolysis and it is the free dye base that passes through the plasma-membrane and appears in the vacuole. Later, however, he abandoned this explanation, as he found that the acetate of rosanilin which is a salt of weak acid and a weak base does not enter the cell any faster than the nitrate or the sulphate. He therefore arrived at a new conclusion, viz., that it is the salt of the basic dye that passes through the plasma-membrane and not the free base. This eliminates the possibility of a chemical reaction and emphasizes more his view that permeability really means physical solubility in the plasma-membrane.

But in reality the fact that the acetate of rosanilin does not seem to pass through the plasma-membrane any faster than the nitrate or hydrochloride does not conflict with his original hypothesis that it is the free base to which the cell is really permeable. His experiments on permeability were not by any means quantitative. He would measure the time required for the appearance of the dye in the vacuole but not the intensity of color which perhaps, could not be measured. One hundred drops of phenolphthalein, for instance, would not produce more coloration in an alkaline solution than ten drops. The work of

[18] Overton, E., Studien über die Aufnahme der Anilinfarben durch die lebenden Zellen. Jahrb. f. Wiss. Bot. **34**: 669–701. 1899–1900.

[19] Overton, l.c.

[20] L.c.

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Harvey[21] tends to corroborate Overton's original free base hypothesis. He found that basic dyes can not enter the cell in the presence of acids and that certain acid dyes enter the cell only in an acid solution. His explanation of the phenomenon is based on the acceptance of Overton's free base (or free acid) hypothesis—in the presence of an acid, for instance, the hydrolysis of a weak base is prevented. On the other hand, he found that the strong alkalies enter the cell only when it is injured by them. This would again fall in line with Overton's view that permeability is a phenomenon of solubility, for if there were some kind of a chemical combination at play, strong alkalies would pass through the plasma-membrane more readily than the basic dyes. It seems however impossible that the chemical nature of a strictly chemical group which is singled out by a certain behavior common to that group only, should not be associated in any way with that behavior. If only bases are capable of passing through the plasma-membrane some corresponding chemical combination would suggest itself very strongly. But how about the behavior of the strong alkalies recorded by Harvey? It is possible that the weak bases hydrolyze and recombine repeatedly until they pass through the plasma-membrane and reach the vacuole while the strong bases enter into chemical combination with the substances of the membrane of the superficial layers of the protoplasm, become fixed, and are unable to pass any further. Another possible explanation is that the basic properties of a dye do not account (as was suggsted by Lepeshkin[22]) for the entrance of the dye, but for its accumulation in the vacuole, due to the fact that the bases enter in combination with the acids of the cell sap.

Overton's lipoid hypothesis has really not deserved the broad popularity which it has received among physiologists. On a stricter examination, it is found to be entirely speculative and based only on a parallelism between permeability of the cell to

[21] Harvey, E. N., Studies on the permeability of cells. Journ. of Exp. Zoölogy **10**: 507–566. 1911.

[22] Lepeshkin, W. W., Zur Kenntniss der Chemischen Zusammensetzung der Plasmamembrane Ber. d. deut. Bot. Ges. **29**: 247–261. 1911.

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certain substances and their solubility in the lipoids. This parallelism may be a mere coincidence. Thus it was found by Traube that the lipoid-soluble substances lower the surface tension of a solution and enter the cell in accordance with his theory of osmosis in which the principal part is played by the tendency of a phase of lower surface tension to move into a phase of higher surface tension.[23] The parallelism itself does not seem to be perfect, according to Ruhland[24] who found for instance, that malachite green and thionin which are only sparingly soluble in lipoids and methylene green which is absolutely insoluble in them enter the cell very easily while rhodamin which is very soluble in lipoids does not seem to penetrate the cell at all. There is besides some intrinsic contradiction in Overton's hypothesis as it stands. Nathanson[25] has shown that the compounds of cholesterin which were substituted by Overton in his theory for cholesterin itself in order to account for the permeability of the cell to water, become on swelling permeable to lipoid-insoluble substances also.

Nathanson[26] has offered a modification of Overton's lipoid hypothesis. According to him, the lipoids of the plasma-membrane are represented by substances like cholesterin which are entirely impermeable to water. The plasma-membrane, however, does not represent a continuous envelope of lipoids, as it is supposed by Overton, but a mosaic of protoplasm and cholesterin, the latter filling in the interstices in the former. The cholesterin in the plasma-membrane conditions the permeability of the cell to such substances as dyes, narcotics, etc.; only those which are soluble in it enter the cell. The passage into the cell of such substances is entirely physical in nature and continues till equal concentration is reached in the outside medium and within the cell. The protoplasmic parts of the membrane condition the permeability of the cell to water to certain neutral salts and to other lipoid-insoluble substances

[23] Harvey, l.c.

[24] L.c.

[25] Nathanson, A., Über die Regulation der Aufnahme Anorg. Salze, etc. Jahrb. f. Wiss. Bot. **39**: 608–644. 1903–04.

[26] L.c.

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which are known to find their way into the cell. The entrance into the cell of these substances, in contradistinction to lipoid-soluble substances is physiological in character, depending upon the regulatory power of the cell. No equalization of concentration is reached within and outside of the cell but a certain equilibrium is established between the two concentrations.

The regulatory power of the cell is, according to Nathanson, of such a nature that it allows of exosmosis of a substance, dissolved in the cell sap, toward a higher concentration. Thus he found that when a cell is transferred from a solution of a higher concentration into a solution of a lower concentration, exosmosis from the cell to the medium takes place till a new equilibrium is established, even when the concentration of the new solution is greater than that of the cell sap. The explanation suggested by Nathanson is that different concentrations of the outside medium affect the permeability of the plasma-membrane in a different manner. This, however, could only explain the establishment of an equilibrium between the concentration of the cell sap and that of the outside solution but would not explain the diffusion of a dissolved substance in the direction of a higher concentration, as it is hard to conceive that permeability should be different with reference to exosmosis than endosmosis. Nathanson's results could, perhaps be explained on the assumption that there is a certain solubility ratio for the substances in question between the cell sap and water, or that the dissolved substances enter into chemical combinations with the substances of the cell sap which are subject to the law of mass action. On the whole, however, one must agree with Ruhland[27] that the experimental methods used by Nathanson are too crude for his results, with reference to the regulatory power of the cell to be considered reliable.

The mechanism of exchange with reference to lipoid-insoluble substances is, according to Nathanson,[28] somewhat analagous to that of an artificial semipermeable membrane. He assumes that there is a certain affinity between the membrane and water

[27] L.c.
[28] L.c.

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which permits the latter to pass when there is a difference in osmotic pressure outside and inside of the cell. To the water soluble substances, he believes, is applied the principle of selective permeability. Only those substances enter the cell which are capable of being dissolved in the small particles of water imbibed by the membrane and which possibly have, due to the close union between them and the membrane, a different solvent power than ordinary water. The difference between an artificial membrane and the plasma-membrane according to him is, that the latter is composed of living protoplasm with a regulatory response to internal and external stimuli.

Ruhland,[29] who considers the experiments of Nathanson with reference to the regulatory power of the cell as not sustained and erroneous, does not think that Nathanson's modification helps in any way the lipoid theory, which he considers as not borne out and intrinsically inconsistent. Why, he asks, should the lipoid-soluble dyes pass through the lipoids and not through the protoplasm which is permeable to water, since they are water soluble, and why should not the lipoid insoluble dyes be capable of entering the cell for the same reason?

These questions are to a certain extent justified by the fact that (as he found)[30] the permeability to dyes is not in any way related to the degree of their colloidality. Thus he found that toluylene red hydrochlorid which is moderately colloidal, prume pure which is strongly colloidal and the base toluylene red which is highly colloidal, all enter the cell very rapidly. On the whole, however, his criticism of Nathanson's modification of the lipoid hypothesis is not consistent (as far as it goes) in view of the fact that even artificial membranes possess the property of selective permeability and in view of the fact that Ruhland himself admits the probability of the cell possessing some regulatory power. His two questions by which he intended to reduce *ad absurdum* Nathanson's modification could be answered very simply: the lipoid soluble dyes do not enter through the pro-

[29] L.c.

[30] Ruhland, W., Die Bedeutung der Kolloidalnatur Wasseriger Farbstofflösungen für Eindringen in lebende Zellen. Ber. d. deut. Bot. Ges. **36**: 772–782. 1908.

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toplasm and lipoid insoluble dyes do not enter the cell at all because the protoplasm is selectively impermeable to them.

Nathanson's modification frees Overton's hypothesis from intrinsic contradictions but deprives it of its universality by relegating the lipoids to a position of secondary importance among the factors which condition the diosmotic properties of the cell. It does not meet the arguments brought against Overton's conclusions with reference to the relation between the lipoids of the plasma-membrane and the aniline dyes, does not substantiate these conclusions by any new evidence, and consequently does not eliminate their speculative character.

Lepeshkin[31] considers the plasma-membrane as a polyphasic colloidal solution of various substances, as protein, lipoids, and water, which in the inner layers passes over into an emulsion or perhaps even into a colloidal suspension. The nature of the dispersing phase is entirely unknown. The solution, according to him, possesses only temporary fluid properties as it has a tendency to solidify. The fluid condition of the plasma-membrane is maintained only under normal conditions of metabolism because a prolonged plasmolysis which interferes with certain physiological functions of the cell, causes solidification of the protoplasm even in the absence of the agencies by which it is generally caused. The permeability of the plasma-membrane is conditioned, according to him, by solubility in the dispersing agent. Water passes through very easily. The endosmosis of other substances depends upon their specific solubility in the dispersing agent of the plasma-membrane. Under the influence of various factors the apparent homogeneousness of the limiting plasma layer disappears. The remaining plasma mass also becomes richer in granular protoplasm and the cell loses the property of selective permeability. The process is, as Lepeshkin is inclined to think, a phenomenon of coagulation. The particles of the dispersed phases in the colloidal solution representing the protoplasm are drawn together. The continuity of the plasma-membrane disappears, channels are formed and are filled with the water which was held in colloidal solution in the

[31] L.c. Ber. d. deut. Bot. Ges., 1910.

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dispersing phase and which underwent the same process (was drawn together) as the other colloidal phases in the plasma-solution. These water filled channels are, according to Lepeshkin, the cause of the loss of the property of selective permeability by the cell on the solidification of the protoplasm as they allow the passage of any substance which is soluble in water. He emphasizes the analogy in this respect between the plasma-membrane and the artificial membranes made for the purpose of studying osmotic pressure. The artificial membranes are also solutions which have a tendency to solidify and form water-filled channels, for which reason they are to be kept in constant contact with the membrane forming solution in order to preserve their efficiency.[32]

The coagulation of the plasma-membrane can be obtained, according to Lepeshkin, by means of mechanical force, heating, and use of chemicals.

That the membrane can be coagulated by mechanical force is shown, as he believes, by the behavior of a *Spirogyra* cell under the influence of mechanical pressure which has been referred to. That this is a case of coagulation and not of mechanical dismembering is shown, according to him, by the fact, that the presence of alkalies in unfavorable for the described behavior of the *Spirogyra* thread, while the presence of acids is favorable—exactly as is the case with coagulation by heating.

From the fact that the plasma-membrane is coagulated by heating Lepeshkin draws the conclusion that it contains considerable quantities of proteins, as it is the proteins which are largely coagulated by heat. The behavior of the protoplasm on heating would also tend to show that there is no difference in protein content between the outer and inner layers as they all coagulated simultaneously when the specific temperature is reached. The heat of coagulation is higher than the normal in the presence of alkali and lower in the presence of acids. This is also in conformity with the behavior of proteins which are completely coagulated only in an acid solution.[33]

[32] Pfeffer, W., Osmotische Untersuchungen, pp. 25–26.
[33] Cohnheim, Chemie der Eiweiszkörper, p. 131. 1904.

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Another indication that proteins are present in abundance in the plasma-membrane is found by Lepeshkin in the fact that (as was shown by his experiments) the same concentration of certain organic substances (ethyl alcohol, methyl alcohol, aldehyde, etc.) are required to coagulate the plasma-membrane in *Spirogyra nitida* and *Tradescantia discolor* as is required to coagulate egg albumen.[34]

Already Pfeffer[35] has advanced the theory that the plasma-membrane consists largely of protein in view of the fact that precipitates are formed in the protoplasm when ions of the heavy metals are introduced.

The presence of lipoids in the plasma-membrane is, according to Lepeshkin, proven by experiments of Overton which shows that narcotics which are very sparingly soluble in water are readily taken up by the cell. The presence of lipoids (oil-like substances) in the plasma-membrane is further proven by Lepeshkin himself when he showed that concentrations of certain narcotics which cause coagulation in the plasma-membrane and in egg albumen are inversely proportional to the solubility coefficients of these substances in water and in olive oil.[36]

Lepeshkin's views, with reference to the nature of the plasma-membrane, do not in reality, differ much from Nathanson's, in spite of his proclaimed opposition to him. He agrees with him that lipoids are present in the plasma-membrane and that they do not form a continuous layer. He disagrees with him with reference to the regulatory power of the cell. To Lepeshkin the entrance of substances into the cell is (as it is to Ruhland) a matter of simple diffusion, and any substance which is soluble in the plasma-membrane will continue to pass into the cell until its concentration within the cell and in the surrounding medium is equalized. He disagrees with Overton and Nathanson with reference to the entrance of the dyes into the cell, and

[34] Lepeshkin, W. W., Zur Kenntniss der Chem. Zusammensetsung der Plasma-membrane. Ber. d. deut. Bot. Ges. **29**: 247–261. 1911.

[35] Pflanzenphysiologie, l. c.

[36] Lepeshkin, W. W., Über die Einwirkung Anästhesierender Stoffe auf die osmotischen Eigenschaften der Plasma-membrane. Ber. d. deut. Bot. Ges. **29**: 349–355. 1911.

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ANTAGONISM BETWEEN MANGANESE AND IRON IN THE GROWTH OF WHEAT

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INTRODUCTION

The effect of manganese upon the growth of plants has been the subject of numerous investigations conducted with nutrient solutions and soils, both in the greenhouse and on field plots. Most of the work along this line has been well summarized by Brenchley.[1] It has been found that while salts of manganese are toxic to higher plants if presented in higher concentrations, they also exercise a stimulating effect which is evident at very low concentrations.

Among the investigations which should be especially noted in the present connection is the work of McCool[2] with Canada field peas. He found calcium effective in counteracting the toxic action of manganese in full nutrient solutions when both elements were supplied as chlorides. He also noted mutual antagonism between manganese and the following elements: potassium, sodium, magnesium. When the two were simultaneously supplied as chlorides magnesium was found to prevent chlorosis by manganese. Particularly striking is McCool's observation that manganese was more injurious the more intense the light, the injurious effects in any case being confined mainly to the tops of the plants.

Aso[3] found manganous sulfate to be toxic to barley, wheat and peas grown in water cultures. The addition of ferrous sulfate

[1] Brenchley, Winifred E., Inorganic Plant Poisons and Stimulants. Cambridge, Eng., 1914.

[2] McCool, M. M., The Action of Certain Nutrient and Non-nutrient Bases on Plant Growth II. Memoir No. 2, Cornell Agrl. Expt. Sta., 1913.

[3] Aso, K., On the action of manganese compounds on plants. Tokyo Coll. of Agr. Bulletins 5 : 177–185, 1902–1903.

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counteracted the effect of manganese by delaying the yellowing of the leaves. The different species of plants varied in their response to manganese and their relief by iron.

Fukutome,[4] growing flax on soil in pots, observed similar beneficial antagonism between manganous chloride and ferrous sulfate.

Kelley[5] has described a chlorotic effect in pineapples grown on soils rich in manganese. He attributes the trouble in large part to the absorption of an excess of calcium by the plant and consequent difficulty in the assimilation of phosphorus.

The investigations here briefly reviewed suggested the purpose of the present investigation. While it is well known that manganese can not replace iron in the physiological requirements of the plant it seems possible, to the contrary, that it may seriously interfere with the functions of the latter element. The present investigation is therefore confined to a study of the effects of equimolecular proportions of manganous and ferric chlorides upon the growth of wheat plants in water cultures. The two concentrations employed with each salt, namely: $\frac{M}{1,000}$ and $\frac{M}{100,000,}$ are equivalent to about 1 part per 8000 and per 800,000 parts of solution respectively for manganous chloride ($MnCl_2$) and 1 part per 6000 and per 600,000 for ferric chloride ($FeCl_2$). These concentrations were chosen because they had been found by previous investigators to lie respectively in the region of distinct toxicity and in that approaching stimulating effects alone, with reference to manganese salts.

The study was limited to the antagonistic relations between manganese and iron in the belief that the chlorotic effects due to manganese might indicate interference with the rôle of iron in the production of chlorophyll. Antagonism between these metals having been demonstrated by the investigations here cited, it appeared possible that the degree, if not the direction, of such

[4] Fukutome, Y., On the influence of manganese salts on flax. Tokyo Coll. of Agr. Bulletins 6 : 137–139, 1904.

[5] Kelley, W. P., The function and distribution of manganese in plants and soils. Hawaii Agr. Expt. Sta. Bulletin 26, 1912.

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antagonism might vary with the total concentration of the two elements in question.

EXPERIMENTATION

Wheat seeds were germinated and the seedlings mounted and grown in the manner[6] previously described by one of the writers. Ordinary one pint mason jars were employed exclusively as culture vessels. These were covered with heavy brown wrapping paper to exclude light. Knop's solution of a total concentration of 0.2 per cent, using mono-potassium phosphate but excluding ferric phosphate, was employed as the control nutrient solution. To this were added either manganous or ferric chloride or both, each to the extent of either $\frac{M}{100,000}$ or $\frac{M}{1,000}$ concentration in the finished nutrient solution. For the sake of brevity these concentrations will be referred to hereafter as low and high respectively.

In preparing the stock solutions of these chlorides the assumption was made that freshly opened materials corresponded with the formulas $MnCl_2 . 4H_2O$ and $FeCl_3 . 6H_2O$. The salts of Knop's solution were dehydrated as described in the work last cited. The distilled water was obtained by condensation into a tin-lined tank from a steam heating system.

Six plants were grown in each of duplicate portions of nutrient solution and the solutions were renewed every third day. After two weeks of growth in the solutions photographs were taken, employing an ortho-chromatic filter to give proper value to yellow leaves and thus record chlorotic effects. After three weeks of growth the plants were removed from the supporting stoppers and the roots were washed in running water. The approximate maximum length of roots was then obtained by computing the average length of the two or three longest groups of roots. When but one root was decidedly longer than the rest it was eliminated from the calculation. Tops and roots were

[6] Tottingham, William E., A quantitative chemical and physiological study of nutrient solutions for plant cultures. Physiological Researches 1 : 133–245, 1914.

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then separated, dried at about 98°C. and weighed. In the few cases where plants failed to develop through apparently inherent unfitness such plants were rejected and correction made to the basis of six plants.

SERIES 1

A small-berried, pure strain of spring wheat was employed in this preliminary series. In figure 1 the superior development of plants in the cultures on the low plane of ferric chloride supply is clearly shown. The unfavorable effect of this salt on the high plane, except in respect to color of the tops, is especially prominent. Attention is particularly called to the prevalence of the toxic effect of manganese over iron at the low plane of supply. This is strikingly evident in the color of the tops. The reverse, however, was the case at the high plane of supply. There the influence of iron was the stronger.

Data concerning the yields are presented in table 1. Each value is the average obtained from duplicate jars.

TABLE 1

Yield of six wheat plants grown three weeks in nutrient solutions containing manganous and ferric chlorides

	CONTROL	LOW $MnCl_2$	LOW $FeCl_3$	LOW $MnCl_2$ AND $FeCl_3$	HIGH $MnCl_2$	HIGH $FeCl_3$	HIGH $MnCl_2$ AND $FeCl_3$
Dry tops							
Weight in milligrams	350	490	785	495	360	325	305
Relative to control = 100	100	140	224	142	103	93	87
Dry roots							
Weight in milligrams	230	210	330	230	170	135	145
Relative to control = 100	100	91	144	100	74	59	63
Fresh roots							
Maximum length in millimeters	198	173	200	153	183	63	60
Relative to control = 100	100	87	101	77	92	32	30

From the data of table 1 it can be seen that with respect to growth of roots even the low plane of manganous chloride was toxic. When supplied jointly with ferric chloride it almost completely antagonized the latter. At the high plane of supply, on

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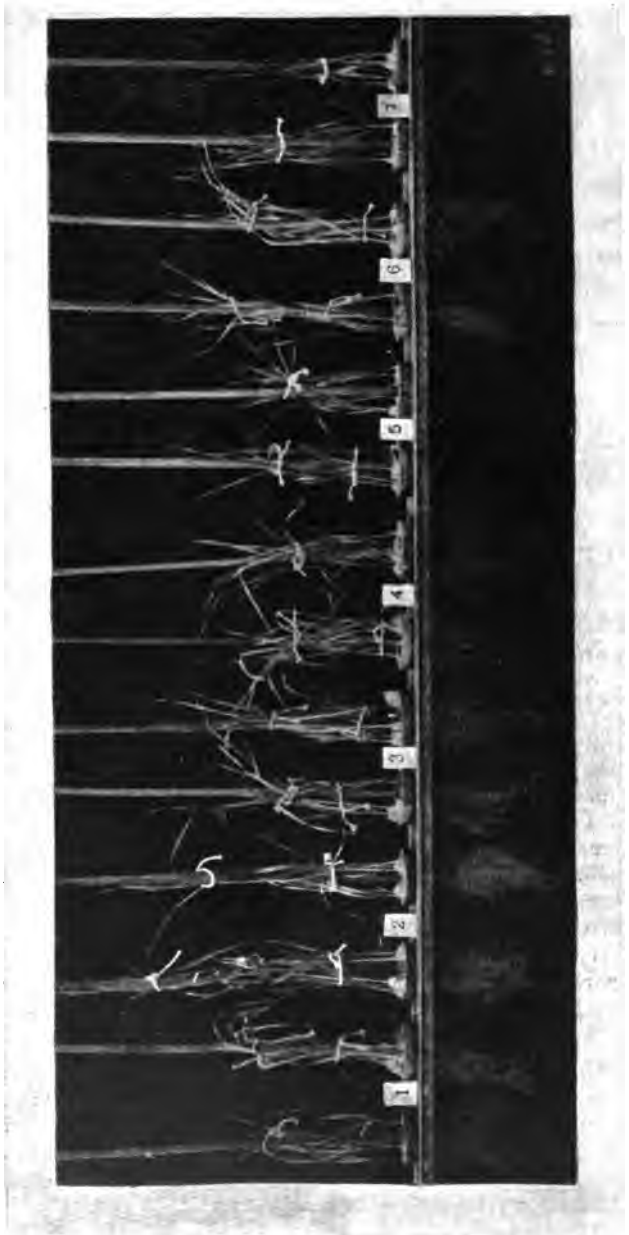

Fig. 1. Effects of manganous and ferric chlorides on young wheat plants. *1*, Control; *2*, M/100,000 $FeCl_3$; *3*, M/100,000 $MnCl_2$; *4*, M/100,000 each, $FeCl_3$ and $MnCl_2$; *5*, M/1 000 $FeCl_3$; *6*, M/1,000 $MnCl_2$; *7*, M/1,000 each, $FeCl_3$ and $MnCl_2$.

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the other hand, ferric chloride was more toxic than manganous chloride and completely antagonized the latter. With regard to the growth of tops the same statements regarding antagonism are true, although manganous chloride was stimulating rather than depressing to this part of the plants. The remarkable stimulating effect of the low plane of ferric chloride suggests that the seed of the variety of wheat here used was notably deficient in reserve iron compounds.

It appeared probable that the disturbances correlated with the high plane of ferric chloride were due to the acidity known to result from hydrolysis of this salt. On this account a second series of cultures was grown with the addition to the nutrient solutions of sodium bi-carbonate ($NaHCO_3$) to maintain neutrality.[7]

SERIES II

In this series a pure strain of Turkey Red wheat, a winter variety, was grown. Two solutions not employed in Series I were introduced here in duplicate. One of these contained sodium bi-carbonate in the concentration $\frac{M}{33,333}$, an amount molecularly equivalent to the ferric chloride of the low plane of Series I. The other was of the concentration $\frac{M}{333}$, equivalent

[7] According to the theory of electrolytic dissociation any salt formed by the union of a strong acid with a weak base will react with water and dissociate (hydrolyze) to form free acid. In a similar manner any salt formed from a strong base and a weak acid will yield free alkali. Strong and weak as here used signify the relative extent to which the acid or base is electrolytically dissociated to free ions, the degree of dissociation being proportional to the strength. By this criterion the strength of acids depends upon the concentration of hydrogen ions in its solutions, while the strength of bases depends similarly upon hydroxyl (OH) ions. It is coming to be recognized, however, that both the molecules and the ions may participate in reactions. The following equations illustrate the production of acidity and alkalinity as applied to the present investigation:

A. $FeCl_3 + 3H_2O = Fe(OH)_3 + 3HCl$; $HCl = H + Cl$.

B. $NaHCO_3 + H_2O = NaOH + H_2CO_3$; $NaOH = Na + OH$.

Equation A leads to acidity because the electrolytic dissociation of ferric hydroxide (not indicated) is very much less than that of hydrochloric acid. Equation B leads to alkalinity in an analogous manner. Thus the two original salts tend to neutralize each other.

See: Stieglitz, Julius, Qualitative Chemical Analysis.
Part 1 : 178–84, New York, 1912.

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to the high plane of ferric chloride. These amounts of the bicarbonate were also added to the nutrient solutions containing the corresponding planes of manganous and ferric chlorides.[8]

It can be seen from figure 2 that the roots developed quite uniformly in this series as compared with Series 1.

The depressing effect of the high plane of ferric chloride previously observed is not evident here. In the appearance of tops, however, the toxic effect of the high plane of sodium bicarbonate is clearly evident. With regard to color of the tops these cultures suffered far less than those of Series 1. This was probably due to a greater store of reserve iron compounds in the seed here employed, for while chlorosis was noticeable in the control culture of Series 1 before two weeks of growth, symptoms of this condition were not evident in Series 2 until the third week of growth, when appreciable chlorotic effects were apparent only in the cultures receiving the high plane of manganous chloride. It will be noticed that this effect was antagonized by the presence of ferric chloride of the same molecular concentration.

[8] The nutrient solutions employed in Series 2 received per liter the following volumes of solutions of various salts of the concentrations indicated:

Control: 13.80 cc. $\frac{M}{2}$ $Ca(NO_3)_2$, 4.90 cc. $\frac{M}{2}$ $MgSO_4$, 3.35 cc. $\frac{M}{2}$ KH_2PO_4, 5.80 cc. $\frac{M}{2}$ KNO_3. To the control solution the following additions were made:

Low sodium bi-carbonate—15.0 cc. $\frac{M}{500}$ $NaHCO_3$

Low manganous chloride—15.0 cc. $\frac{M}{500}$ $NaHCO_3$, 5 cc. $\frac{M}{500}$ $MnCl_2$.

Low ferric chloride—15.0 cc. $\frac{M}{500}$ $NaHCO_3$, 5 cc. $\frac{M}{500}$ $FeCl_3$.

Low manganous and ferric chlorides 15.0 cc. $\frac{M}{500}$ $NaHCO_3$ $\begin{cases} 5 \text{ cc. } \frac{M}{500} MnCl_2 \\ 5 \text{ cc. } \frac{M}{500} FeCl_3. \end{cases}$

High sodium bi-carbonate—15.0 cc. $\frac{M}{5}$ $NaHCO_3$

High manganous chloride—15.0 cc. $\frac{M}{5}$ $NaHCO_3$ 5 cc. $\frac{M}{5}$ $MnCl_2$

High ferric chloride—15.0 cc. $\frac{M}{5}$ $NaHCo_3$ 5 cc. $\frac{M}{5}$ $FeCl_3$

High manganous and ferric chlorides—15.0 cc. $\frac{M}{5}$ $NaHCO_3$ $\begin{cases} 5 \text{ cc. } \frac{M}{5} MnCl_2 \\ 5 \text{ cc. } \frac{M}{5} FeCl_3. \end{cases}$

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Figure 2. Effects of manganous and ferric chlorides on young wheat plants in the presence of sodium bi-carbonate. *1*, Control; *2*, M/33,333 $NaHCO_3$, *3*, M/33,333 $NaHCO_3$ and M/100,000 $FeCl_3$; *4*, M/33,333 $NaHCO_3$ and M/100,000 $MnCl_2$; *5*, M/33,333 $NaHCO_3$ and M/100,000 each, $FeCl_3$ and $MnCl_2$; *6*, M/333 $NaHCO_3$; *7*, M/333 $NaHCO_3$ and M/1,000 $FeCl_3$; *8*, M/333 $NaHCO_3$ and M/1,000 $MnCl_2$; *9*, M/333 $NaHCO_3$ and M/1,000 each, $FeCl_3$ and $MnCl_2$.

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Data of the yields of Series 2 are presented in table 2.

As shown by the data of table 2 manganous chloride on the low plane was toxic to both roots and tops of the plants. This differs from the effect in Series 1, where it stimulated the growth of tops. As in the previous series, but to a less degree, it antagonized the effect of ferric chloride at this plane. However, in harmony with the delayed chlorotic effects, the slight stimulation by low ferric chloride and the less complete antagonism by manganous chloride toward this salt suggest a varietal resistance to the effects of manganese dependent upon a liberal reserve of iron in the seed. On the other hand, the toxic effect of manganous chloride alone is opposed to this point of view.

TABLE 2

Yield of six wheat plants grown three weeks in nutrient solutions containing sodium bi-carbonate and manganous and ferric chlorides

	CONTROL	LOW $NaHCO_3$	LOW $NaHCO_3$ AND $MnCl_2$	LOW $NaHCO_3$ AND $FeCl_3$	LOW $NaHCO_3$, $MnCl_2$ AND $FeCl_3$	HIGH $NaHCO_3$	HIGH $NaHCO_3$ AND $MnCl_2$	HIGH $NaHCO_3$ AND $FeCl_3$	HIGH $NaHCO_3$, $MnCl_2$ AND $FeCl_3$
Dry tops									
Weight in milligrams.....	621	632	453	647	566	260	250	854	725
Relative to control = 100.	100	102	73	104	91	42	40	138	117
Dry roots									
Weight in milligrams.....	221	228	185	249	191	163	117	210	195
Relative to control = 100.	100	103	84	113	87	74	53	95	88
Fresh roots									
Maximum length in millimeters.....	275	233	278	265	295	231	233	260	298
Relative to control = 100	100	85	101	96	107	84	85	95	108

The very serious toxicity of the high plane of sodium bi-carbonate may have depended either upon the disturbed balance of ions attending the precipitation which occurred in all solutions on this plane of the series or upon the specific effects of this salt upon the plant. It is remarkable that the degree of toxicity was but slightly influenced by the added presence of manganous chloride. Contrary to the results of Series 1, high ferric chloride stimulated the growth of tops here. In partial

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harmony with the results of the former series, however, it antagonized the combined effects of sodium bi-carbonate and manganous chloride to a great extent.

REACTION OF THE NUTRIENT SOLUTIONS

In view of the apparent importance of the acidity or alkalinity of the nutrient solution in the regulation of injury, as observed in the preceding experiments, determinations of the hydrogen-ion concentration[9] were made upon some of the solutions there employed. The measurements were made by the colorimetric method of Sorensen,[10] after exposing the solutions for three or four days to a rather uniform temperature of about 20°C. The data, which are presented in table 3, should be considered as approximate only, on account of comparative lack of refinement in the technique applied.[11]

TABLE 3

Approximate hydrogen ion concentration of selected nutrient solutions

	CONTROL	HIGH $MnCl_2$	HIGH $FeCl_3$	HIGH $MnCl_2$ AND $FeCl_3$
Series 1	14	20	300	250

		CONTROL	LOW $NaHCO_3$	HIGH $NaHCO_3$	HIGH $NaHCO_3$ AND $MnCl_2$	HIGH $NaHCO_3$ AND $FeCl_3$	HIGH $NaHCO_3$, $MnCl_2$ AND $FeCl_3$
Series 2	A.	15	10	1.3	0.4	1.3	1.3
	B.	13	13	1.0	0.4	1.0	1.0

[9] It may be desirable to explain here that hydrogen ion concentration and acidity, in the sense in which the latter term is commonly employed, are not always synonymous. They are synonymous only at very low concentrations of some acids, where electrolytic dissociation is complete. In other cases the hydrogen ion concentration is a measure only of the *dissociated*, acid hydrogen atoms. The ordinary method of titration with a standard solution of alkali gives the *total* concentration of acid hydrogen atoms.

[10] Sorensen, S. P. L. Über die Messung und Bedeutung der Wasserstoffionen-Konzentration bei biologischen Prozessen. Ergebnisse der Physiologie **12**: 393-532, 1912.

[11] The unit of measurement is 1 gram of hydrogen ion per 10 million liters of solution or $\frac{N}{10,000,000}$. Water, which is taken as the basis of neutrality, has this concentration of hydrogen ion at 21°C. Sodium alizarin sulfonate was employed as the indicator in Series 1 and 2 A. Neutral red, more sensitive near the neutral point, was employed in Series 2 B.

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From the data of table 3 it is clear that the injurious effect of the high plane of ferric chloride in Series 1 was correlated with high acidity of the nutrient solutions. It is also clear that while the low plane of sodium bi-carbonate had slight effect toward neutrality the high plane of this salt accomplished the purposed result. Accepting the conclusion of Hartwell and Pember[12] that a considerable range of acidity to alkalinity around the neutral point is favorable for the growth of wheat it would appear that the toxic effect of the high plane of sodium bi-carbonate in Series 2 must be ascribed directly to causes other than the production of neutrality in the nutrient solution. It seems desirable, however, to investigate this point in relation to the effects of toxic elements on the basis of the concentration of hydrogen or hydroxyl ion.

SUMMARY

In view of the limited amount of experimental evidence here presented the drawing of broad and final conclusions is unjustified. The following concluding statements seem, however, to be in order:

1. The effects of manganous and ferric chlorides upon the growth of young wheat plants in water cultures depend partly upon the variety of wheat employed.

2. The amount of reserve iron in the seed is probably one of the important factors determining the response of wheat plants to supplies of iron and manganese salts.

3. At the concentration $\frac{M}{100,000}$ superimposed upon iron-free Knop's solution of 0.2 per cent concentration manganous chloride exerted stronger effects than ferric chloride upon the growth and color of the varieties of wheat employed here.

4. At the concentration $\frac{M}{1,000}$, superimposed upon iron-free Knop's solution of 0.2 per cent total concentration ferric chloride exerted stronger effects than manganous chloride upon the growth and color of the varieties of wheat employed here. This

[12] Hartwell, B. L. and Pember, F. R., The relation between the effects of liming, and of nutrient solutions containing different amounts of acid, upon the growth of certain cereals. Rhode Island Exp. Sta. Ann. Rept. **20**: 358–380, 1907.

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relation held whether or not the acidity tending to develop by hydrolysis of ferric chloride was prevented.

5. Although the lower plane of concentration upon which iron and manganese were employed here approaches that probably obtaining in the average water extract of soils, the application of the preceding conclusions to field conditions would be clearly unjustified. A greater variety of component salts and various other conditions might modify the effects of the elements in question in soil cultures as compared with water cultures. The soil phase of the problem therefore calls for further investigation.

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THE EFFECT OF VANILLIN AND SALICYLIC ALDEHYDE IN CULTURE SOLUTION AND THE ACTION OF CHEMICALS IN ALTERING THEIR INFLUENCE*

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A study of the effect of organic compounds on plant growth in distilled water, in nutrient culture solutions, and in soil in pots and in the field has been made by this laboratory and the results reported from time to time. An interesting development in this line of work is the experiments bearing on the effect of the inorganic salts, such as sodium nitrate, calcium phosphate, potassium sulphate, calcium carbonate and the manganese salts in altering the action of certain of these organic compounds on plants.

With wheat plants in culture solutions vanillin and dihydroxystearic acid have their harmful effects greatly diminished by the addition of sodium nitrate or by calcium carbonate, whereas their harmfulness remains unimpaired by phosphate or potash fertilizers. Nitrate is an oxidizing substance and it has been shown that root oxidation is increased greatly by its use, whereas vanillin decreases root oxidation and is capable of being oxidized. The effect of these chemicals is to promote biological processes that change or destroy these organic compounds. Quinone has its harmful action reduced by potash salts; it is an active oxidizing substance, while potash reduces root oxidation. Thus these two substances antagonize each other in their effects. On the other hand, the harmful effects of cumarin and salicylic aldehyde are partially remedied by phosphates, and calcium carbonate also alters the effects of salicylic aldehyde.

Field experiments also show that the harmfulness of vanillin

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is altered by nitrate fertilizers and that of salicylic aldehyde by phosphates, and the action of both compounds is affected by lime.[1]

With wheat growing in nutrient solutions the absorption of salts is affected differently by different organic substances.[2] In the experiment with which this paper deals the effect of vanillin on cowpeas and its effect on the absorption of nutrients from the solution is determined. The action of manganese in altering the effects of both vanillin and salicylic aldehyde was studied and the results are reported here.

THE EFFECT OF VANILLIN ON COWPEAS IN NUTRIENT SOLUTIONS OF DIFFERENT COMPOSITIONS

An experiment growing cowpeas in nutrient solutions was made in which the effect of vanillin was studied. The solutions were composed of calcium acid phosphate, sodium nitrate and potassium sulphate, used singly and in combinations. It was found that in some of these nutrient solutions the vanillin was more harmful than in others. Culture jars holding 250 cc. of solution were used, and two cowpea plants were grown in each jar. The plants were germinated in sand and when about 1 inch high were put in the nutrient solution. The culture solutions, as stated above, were composed of calcium acid phosphate, sodium nitrate and potassium sulphate, in amount of 80 parts per million total of P_2O_5, NH_3 and K_2O. These solutions were changed every fifth day; the old solutions were replaced by new four times during the experiment. They were analyzed to determine the amount of phosphate, nitrate and potash removed by the plants. In this way the effect of vanillin on the metabolism of plants was studied. The peas grew for 21 days, from June 17 to July 8. The results are given in table 1. The composition of the culture solutions is given in the second, third, and fourth columns. The green weights of the plants grown

[1] Skinner, J. J., and Noll C. F., Field test on the action of fertilizers on soil aldehydes Jour. Amer. Soc. Agron. **8**: 273. (1916).

[2] Schreiner, O., and Skinner, J. J., The toxic action of organic compounds as modified by fertilizer salts. Bot. Gaz. **54**: 31. 1912.

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in the solutions without vanillin are given in the fifth column, and with 100 parts per million of vanillin in the sixth column. The absorption of the nutrient salts is given in the remainder of the table.

TABLE 1

Effect of cowpeas in nutrient solution with and without vanillin. (100 p.p.m.) June 17–July 8

NO.	COMPOSITION OF CULTURE SOLUTION			GREEN WEIGHT OF CULTURES		NUTRIENT ABSORBED					
						P_2O_5		NO_3 stated as NH_3		K_2O	
	P_2O_5	NH_3	K_2O	without vanillin	with vanillin	without vanillin	with vanillin	without vanillin	with vanillin	without vanillin	with vanillin
	p.p.m.	*p.p.m.*	*p.p.m.*	*grams*	*grams*	*m.g.*	*m.g.*	*m.g.*	*m.g.*	*m.g.*	*m.g.*
1	80	0	0	1.37	1.10	16.0	13.2				
2	64	8	8	3.57	2.50	15.3	13.1	8.0	7.5	4.9	4.0
3	48	16	16	4.87	3.97	12.1	7.3	12.2	8.9	12.2	6.4
4	32	24	24	5.37	3.55	10.7	7.1	14.6	13.2	17.5	17.5
				15.18	11.12						
5	0	80	0	2.20	2.70			25.5	24.6		
6	8	64	8	3.52	3.40	1.8	0.6	15.3	14.6	3.5	2.3
7	16	48	16	5.02	4.95	3.4	3.4	12.9	16.8	12.0	8.0
8	24	32	24	4.55	4.30	10.4	7.9	17.4	13.1	12.0	15.0
				15.29	15.35						
	0	0	80	1.85	0.80					30.2	8.0
9	8	8	64	4.67	4.05	2.1	3.8	8.0	7.7	25.6	23.0
10	16	16	48	5.47	3.70	3.8	4.5	12.1	11.8	24.0	19.0
11	24	24	32	5.95	3.00	8.7	5.3	16.3	10.8	28.5	11.5
12											
				17.94	11.55						
Total				48.41	38.12	84.3	66.2	142.3	129.0	170.4	114.7
Per cent decrease in vanillin culture					29		21		10		33

The green weight was reduced by the vanillin in each culture except No. 5. When the cultures are grouped as in the table according to their composition it is seen that the vanillin is least harmful in those cultures which are composed principally

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of nitrates. Cultures Nos. 1 to 4 are composed principally of phosphate; Nos. 5 to 8 principally of nitrates, and Nos. 9 to 12 principally of potassium. The total green weight of the high phosphate cultures (Nos. 1 to 4) was 15.18 grams in the solutions without vanillin, and 11.12 grams with vanillin. In the high nitrate cultures (Nos. 5 to 8) the weight without vanillin was 15.29 grams against 15.35 grams for the cultures with vanillin. In the high potash cultures (Nos. 9 to 12) the weight without vanillin was 17.94 grams, against 11.55 grams for the cultures with vanillin. It is apparent that in the solutions composed principally of nitrate the vanillin had practically no effect, and in culture No. 5, composed of all nitrate, the growth in the vanillin culture was larger than in its control.

The growth of the cowpeas without and with vanillin in solution Nos. 3, 7, and 11 is shown in figure 1. Here it is shown that

Fig. 1. Effect of vanillin on cowpeas in nutrient solutions of different compositions. (No. 3, nutrient solution containing 48 p.p.m. P_2O_5, 16 p.p.m. NH_3, 16 p.p.m. K_2O. No. 3a, Same + 100 p.p.m. vanillin. No. 7, nutrient solution containing 16 p.p.m. P_2O_5, 48 p.p.m. NH_3, and 16 p.p.m. K_2O. No. 7a, Same + 100 p.p.m. vanillin. No. 11, nutrient solution containing 16 p.p.m. P_2O_5, 16 p.p.m. NH_3 and 48 p.p.m. K_2O. No. 11a, Same + 100 p.p.m. vanillin).

the growth in solution No. 7, composed of 16 parts per million P_2O_5, 48 parts per million NH_3 as nitrate, and 16 parts per million N_2O, is as good in the solution with vanillin as in its check, which contains no vanillin.

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believes that they diffuse through the water which is held, as he claims to have shown, in solution in the plasma-membrane. Any dye soluble in water regardless of its solubility or insolubility in lipoids will, according, to him diffuse into the cell. Overton's observations with reference to the permeability of the cell to dyes concern themselves, according to him as well as according to Ruhland[37] only with the accumulation of these dyes in the cell. The water-soluble dyes which are classed among those to which the cell is impermeable, in reality enter the cell but do not accumulate. The fact that only basic dyes were found by Overton to penetrate into the cell lends, according to him, support to his view, as the basic dyes form compounds with the organic acids found in the cell sap and precipitate out. With reference to the few acid dyes which were definitely found by Pfeffer to be incapable of entering the cell, he found that they form distinctly colloidal solutions which pass with difficulty through the cell wall and with still more difficulty through the protoplasm even after the cell is killed by heating.

As a proof against Nathanson's view that the aniline dyes enter the cell through the lipoids, Lepeshkin considers the fact that, (as was shown by him) aniline dyes which are more soluble in water than in certain narcotics enter the cell with more difficulty in the presence of these narcotics. This would, according to him, tend to show that all substances to which a cell is permeable enter through the same way and that there are no different passage ways for aniline dyes and mineral salts, for instance.[38]

This argument as well as Lepeshkin's opposition to Nathanson's conception of the plasma-membrane in general is somewhat inconsistent. The principal point in Nathanson's modification of Overton's lipoid-hypothesis is that the lipoids do not form a continuous layer in the plasma-membrane. Lepeshkin holds the same view. As to the existence of different passage ways in the plasma-membrane for different substances Lepeshkin recognizes the same principle, having assumed that the narcotics sparingly soluble in water enter through the lipoid components

[37] L.c., Jahrb. f. Wiss. Bot. **46**.

[38] L.c., Ber. d. d. Bot. Ges. **29**: 247–261. 1911.

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of the plasma-membrane. Why not assume the view point of Nathanson, viz., that the aniline dyes enter by the same passage way? The fact that the aniline dyes are soluble in water need not be considered since the aniline dyes referred to by Overton are so much more soluble in lipoids than in water. Their solubility in lipoids is, perhaps, another condition for their accumulation.

It is safe therefore to state that there is no essential difference between Nathanson's conception of the plasma-membrane and that of Lepeshkin. The latter has only gone a step farther by trying to get an insight into the physical state and chemical composition of that part of the plasma-membrane which the former simply terms as protoplasm. The essential difference in the views of the two investigators is their relation to the regulatory power of the cell as it is understood by Nathanson, but this difference does not follow directly from their respective conceptions of the plasma-membrane.

It is, however, very evident that both investigators relegate the lipoids of the plasma-membrane to a secondary position among the factors conditioning the selective properties of the cell with reference to permeability.

SUMMARY

(1) The subject of the existence of special plasma-membranes is very little discussed in the literature and the meager evidence at our disposal is too indefinite and too indirect to enable us to draw any conclusious.

When the term plasma-membrane is used in the literature it may refer to the entire cytoplasm as well as to a special membrane.

(2) The discussion of the subject of selective permeability of living cells and of the mechanism of diosmosis is entirely speculative and the evidence offered in favor of any of the various theories advanced is too indirect to allow of any conclusions.

(3) The lipoid theory as it has been formulated by Overton is intrinsically contradictory, and the modifications of Nathan-

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son and Lepeshkin relegate the role of the lipoids as factors conditioning the selective permeability of cells to a secondary place.

(4) There is no adequate method of testing the permeability of living cells. The observational methods (appearance of color, change of color, appearance of precipitates) are limited only to certain classes of substances, mostly unessential, and are conclusive only with reference to positive results (when permeability is demonstrated), but leave the matter unsettled when negative results are obtained. The plasmolytic method leads to results so contradictory that it can hardly be used as a reliable test of permeability in all cases.

(5) It is possible that the universally accepted explanation of the plasmolytic phenomena is not correct in spite of its plausibility and conformity to so many known facts. It is possible that there are factors involved in the failure to recover from plasmolysis other than the inability of the substance in solution to enter the cell. It is possible, for instance, that the substances which produce plasmolysis and are at the same time known to find their way into the cell produce certain reversible changes in the components of the plasma-membrane which prevent the cell from regaining its original volume notwithstanding the equalization of the concentration within and without of the cell.

The writer acknowledges his indebtedness to Dr. Lewis Knudson, upon whose recommendation this article was written, for valuable information with reference to the bibliography on the question.

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THE ORCHIDS OF HAWAII

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The Hawaiian flora has long been the object of scientific interest and investigation. The Hawaiian Archipelago has a unique biogeographic situation in its great remoteness from the continental land areas. Its ecologic zones and districts are strikingly diverse. Certain large plant groups are entirely absent; others are well represented and highly developed. These and many other features that might be enumerated have all combined to give the plant life of Hawaii a position of great and unique scientific value among the insular floras.

The popular impression that tropical islands are veritable conservatories of choice and beautiful orchids receives a shock in Hawaii. There are only three orchids in the Hawaiian woodlands, and these are inconspicuous and by no means abundant. One species is restricted to the rarely-visited summit bogs. The other two, although occurring in the lower humid forests, would easily pass unnoticed by any save the professional botanist. Since the first explorations of the Hawaiian forests, botanists have repeatedly commented upon the paucity and insignificance of the orchid flora.

Recent geological studies of the Hawaiian Archipelago are placing emphasis upon the great antiquity of this island group. There is much evidence to substantiate the view that the present islands are but the remnants of a once vastly larger land area, that has almost wholly subsided beneath the ocean. This is in accord with evidence obtained from many other parts of the great Pacific region. It is entirely possible that the Hawaiian region was isolated through submergence long before the final burst of orchid migration and specialization in Malaya and the South Pacific.

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The present meager representation of this large, distinctive, and highly specialized family by only three humble species probably points to one of two hypotheses. These may be the vestiges of a much larger primitive orchid flora that has been wiped out by profound and long-continued ecologic changes in the environment. This view would coincide with evidence from other plant and animal groups in the Hawaiian biota. On the other hand, Hawaii's orchids may be mere fortuitous stragglers, that through some unknown migration agency were carried to this isolated island world, and during a long time interval have evolved as endemic species. It is of some significance that none of the three genera represented are endemic, but occur in many other parts of the world.

The genus *Anoectochilus* has a single endemic representative in Hawaii. The generic name, from the Greek, refers to the open or deflected lip of the flower. The genus comprises about eight species and extends from southern India across Mal ya and northeastward across Polynesia. Hawaii is the northernmost Pacific limit of this group. These quaint little orchids are terrestrial in habitat. They are characterized by a creeping, leafy rhizome.

Our one species, *A. Sandwichensis* Lindl., has a decumbent rhizome 1.5 to 3.0 dm. long. This is round in cross-section, succulent, purple-red in color, rooting freely at the nodes, and leafy throughout. The four to six beautiful leaves form a basal cluster or rosette, and constitute the chief beauty of this little orchid. They are rich velvety dark green in color, with a lovely iridescent gloss when fresh. This delicate sheen rapidly disappears when the plant or leaf is plucked. The leaves are ovate or oblong, 4 to 9 cm. in length, and 2 to 5 cm. in breadth, on petioles of 1 to 2.5 cm. The petioles expand at the base into a loose saccate sheath. The blade is membranaceous in texture, and the veins form a delicate reticulate pattern against the rich velvety body of the leaf. It is of interest to note that several species of *Anoectochilus* are cultivated for their handsome metallic-veined foliage; none of this genus has ornamental flowers. One species, *A. regalis* of Java, has exquisite leaves

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with a wonderful venation of golden tracery against a bronze-green background. Other species have silver veins.

The flowers of the Hawaiian *Anoectochilus*, like those of the other members of the genus, are neither showy nor remarkable. The many-flowered terminal spike rises to a height of 14 to 16 cm. Near its base are several empty bracts. The flowers are yellow, and are sometimes marked with a few pinkish spots. The most conspicuous feature of the flower is the long two-lobed blade. The following description, modified and revised from Hillebrand[1] will present the details of the floral structure of this modest Hawaiian orchid:

Sepals: Spreading, broadly ovate, and united at the base. The upper ones are united with the petals and form a three-pointed "helmet." The lateral ones are oblique, ovate-oblong. Length of perigone, 8 mm.

Lip: Adnate to the foot of the column; spreading; deflected; saccate at the base; 10 to 12 mm. long. It is prolonged into a narrow, channeled, entire or denticulate *claw*, which is broadly expanded and deeply 2-lobed at the apex.

Column: Short, curved above and emarginate; with two large globose callosities in front of the projecting rostellum; bilamellate below the stigma.

Anther: Terminal, free; incumbent on the apex of the column; persistent, bilocular; finally becoming erect.

Pollinia: Two lobed; consisting of rather large, easily-separable granules. The pollinia are prolonged into short caudicles which are attached to a common viscid gland.

Capsule: Conspicuously three-ribbed; 1 cm. long.

Dr. Hillebrand mentions a variety which he designates *beta*, with a finely fringed claw. This however is rare and of doubtful status, as he himself states that both types of flowers occur in the same clump of plants. It has not been found by the writer.

This inconspicuous orchid grows here and there in the humid portions of the lower forest zone of all the islands, up to an elevation of 1200 to 1500 feet. It prefers moist, shady places, such as ravines, wooded valley slopes, and the groves along streambeds. It is nowhere abundant, and is generally solitary,

[1] Hillebrand, William, Hawaii's greatest botanist; a German physician who lived for many years in Honolulu; the manuscript of his great Flora of the Hawaiian Islands was completed just two months before his death, and was published posthumously (1888). The work is out of print, and very scarce.

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although occasionally small clumps containing four to six or more plants may be found.

Occurring in the same habitats as *Anoectochilus*, namely the humid lower forest zone of all the islands, is the single native species of *Liparis*, *L. Hawaiiensis* Mann. Although not infrequent in the lower forest, this epiphytic orchid also inhabits the middle forests, and is to be found on slopes and ridges much higher than those occupied by *Anoectochilus*. The Hawaiian "Twayblade" grows chiefly on the horizontal mossy branches of the old trees, and in humus-filled crotches, but occasionally is met on mossy ground in the rain forest. In such situations it grows not in the soil proper, but in the dense vegetative covering of mosses, liverworts, lichens, and lesser ferns.

The genus *Liparis* comprises over 120 species, scattered over the tropic and temperate regions of the entire world. The generic name means fat or shining, and refers to the shining fleshy leaves. In our species the stems are thickened at the base into small, oval pseudo-bulbs, sheathed by scales. There are two large basal leaves, hence the English name "twayblade." The stem also bears a few leaf-like scales. The basal leaves are glossy, ovate or oblong, 8 to 25 cm. long by 3 to 9 cm. broad. The apex is somewhat obtuse; the base is contracted and nearly petiolate. The numerous fine parallel veins spring from the entire length of the midrib.

The inflorescence is tall but scarcely showy. The angled scape rises to a height of 1.3 to 4.5 dm. It bears three to ten delicate greenish-white flowers in its upper portion; the lower part is naked. The twisted pedicels are 6 or 7 mm. long; the ovate bracts are about half as long as the pedicels. A detailed characterization of the flower, revised from Hillebrand, follows:

Sepals: Ascending; linear or narrow lanceolate; 8 to 10 mm. long.

Petals: A little shorter than the sepals; filiform; spreading.

Lip: As long as the petals; thin membranaceous; ascending below and channelled or folded, but without tubercles. The lip terminates in a flat, entire oblong or obovate blade.

Column: Erect, incurved, slender; winged at the top; about half as long as the sepals, and continuous with the ovary.

Anther: Terminal, lid-like.

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Pollinia: Waxy, without caudicles or stigmatic glands; in two pairs; attached by their summits, but spreading laterally into the two pollen-sacs.

Capsule: 10 to 15 mm. long, obovate-oblong and prominently ribbed.

Hawaii can boast but a single representative of the large and well-known genus *Habenaria*, popularly known as the Butterfly Orchids. This group consists of about four hundred species of terrestrial leafy orchids, widely distributed in temperate and tropical regions throughout the world. The generic name, from the Greek, a thong or strap, refers to the conspicuous floral lip or to the long spur. The spur is a nectary, and many species are also very fragrant.

The Hawaiian species, *H. holochila* Hilleb. is endemic and peculiar to the remarkable summit bogs that occur on a number of the Hawaiian mountains. These bogs are situated at an elevation of 3000 to 6000 feet, in the cloud belt, and are excessively wet. They comprise a distinct ecologic district. Their peculiarities have been described by the writer in a paper in the American Botanist[2] and his reference list of their highly precinctive flora is to appear shortly in the Hawaiian Forester.

Habenaria holochila grows in very boggy soil. The slender tuberous rhizome is subterranean, erect, and cylindric or spindle-form. Around its summit is a crown of numerous small fleshy roots. At the termination of its season of growth and flowering, the tuber decays, but the plant is renewed perennially by the development of a new tuber by the side of the exhausted one.

The erect stem is leafy throughout, and is terminated by a spike of inconspicuous green flowers. The stem is hollow, and like the tuber, is renewed seasonally. The remains of the old dead stems may be found amongst the basal leaves as a mature plant.

There are five to ten leaves, the basal ones largest, the upper ones modified as sheathing scales. The leaves are oval or elliptic-oblong, membranaceous, 10 to 15 cm. long by 4 to 5.5 cm. broad; apex acuminate; base sheathing. There are three to five primary veins and six to fourteen secondary veins.

[2] Vegetation of the Hawaiian Summit Bogs. In press.

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The dull green floral spike is disappointingly mediocre to anyone who is familiar with the beautiful fringed orchids of the northeastern states. The flowering stem attains a height of 3.0 to 7.5 dm. The bracts which subtend the flowers, one below each flower, are longer than the blossoms, and obscure them. The lower bracts are lanceolate and foliar; the others gradually diminish in size towards the apex of the spike.

The detailed description of the flower is modified from Hillebrand's original description:

Sepals: Coriaceous, subequal, broadly ovate, 4 mm. long, all converging.

Petals: As long as the sepals; converging, abruptly tapering from a broad, sessile, uneven-sided basal part to a slender apex. The apex is recurved, linear, and truncate or emarginate.

Lip: Thick, linear, entire, (hence the specific name *holochila*); truncate, ridged in the middle, curved ascending. The lip is nearly as long as the sepals, and is provided with a thick, club-shaped *spur*, longer than itself, and only a little shorter than the ovary.

Column: Very short; sessile; with a short rostellum; erect under the anther.

Anther: Terminal but adnate to the face of the column; pollen-sacs nearly parallel.

Pollinia: Two, granular; the caudicles terminating in naked viscid glands distant from each other and not imbedded in cells of the 2-lobed stigma. These glands are so arranged as to readily adhere to the head of any visiting insect.

Capsule: 12 to 14 mm. long; seeds oblong, margined.

It is to be regretted that nothing can be reported as to the mechanics of cross-pollination in the Hawaiian orchids. Insects are by no means abundant in the native forest, as compared with those of continental regions. As with the plant series, so with the insect series, there are many important groups either entirely absent from the Hawaiian fauna, or only meagerly represented. The insect fauna is surprisingly lacking in the forms commonly associated with cross-pollination phenomen in other countries. There are no data at hand to indicate accurately the insect agencies in the pollination work. Possibly a certain amount of close pollination takes place, as mature capsules are not uncommon. The biologic relationships of Hawaii's three endemic orchids offer an attractive problem.

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BOOKS AND CURRENT LITERATURE

TRANSPIRATION OF CORN.—A recent comprehensive study by Kiesselbach[1] is a very material contribution to our knowledge of the water relations of plants as a factor in crop production. Laboratory methods of study on transpiration were applied to corn plants grown in large potometers in the field. The yield from these plants was entirely normal when compared with plants grown under usual conditions, so the results of this study are to be regarded as far reaching in giving a correct understanding of the principles involved in the use of water as influenced by cultural practices.

In periods of drouth on days of extreme temperature, a single corn plant may transpire as much as 10 pounds of water in twenty-four hours. Transpiration may be 300 to 400 times greater one day than the following day. Fully one-half of the total water used by the plant occurs in the four or five weeks' period following its maximum development of leaf area. It was found from the results of three years' tests, that the lowering of the water content of the soil below the optimum was accompanied by 37.3% decrease in stalk yield, 28.5% in year yield and 30.7% in total dry matter. The increase in soil moisture content above the optimum was accompanied by a reduction in stalk yield of 11.3%, in ear yield of 27.1% and in total dry matter of 16.7%.

Increase in fertility of the soil by the application of manure was found to reduce the water requirement for grain production. A range in variation of from 230 to 296 pounds of water per pound of dry matter existed in the eleven varieties of corn tested. The so-called drouth-resistant varieties of corn possessed practically the same water requirements per pound of dry matter as did the other varieties.

Considerable variation existed in the different varieties of corn in thickness of leaf and number of stomata per unit of leaf area with no apparent correlation, however, between these anatomical differences and the transpiration rate per unit of dry matter. The total area of the stomatal apertures when open occupied 1.52% of the entire leaf area.—F. A. WOLF.

[1]Kiesselbach, T. A. Transpiration as a Factor in Crop Production. Neb. Agr. Ex. Sta. Res. Bull. **6**: 1–214, 1916.

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NOTES AND COMMENT

The forest pathologists of the eastern United States have their hands very full at the present time. The chestnut blight peril has been overshadowed by the spread of the much-dreaded white pine blister rust (*Cronartium ribicola*), which promises to far exceed the former in its ravages. The rust attacks five-needle pines, and like certain of the grass rusts, must reach a second host in order to complete its life-cycle. The second host in this case may be either the gooseberry or the currant, wild or cultivated. The aecidiospores developed on the pine host are spread in May and June, and the resulting mycelium on gooseberry and currant bushes produces a yellow rust (uredospores) on the abaxial surfaces of the leaves. Spores of the yellow rust are shed from the first of June to the end of the summer and carry on further infection of the second host over considerable distances (as far as 20 miles). In late July another type of spore (the teliospore) which must reach the white pine in order to germinate, appears on the same mycelium that produced the uredospores. The mycelium in the pine now undergoes a period of "incubation" varying in length from less than one year to several years, then forms the white, blister-like aecidia which appear on the surface of the bark and give the common name to the disease.

Up to date the white pine blister rust has appeared in thirteen states and is now as far west as Minnesota. Estimates of government foresters place the value of mature standing white pine endangered in the eastern and western forests of the United States at $186,000,000 and $240,000,000 respectively. Infected nursery stock is the principal agent of interstate dispersal, so that by prompt action the western forests may yet be saved. Measures recommended by competent foresters and pathologists for checking the disease are: destruction of infected trees; quarantine of nurseries in infected districts; rigid government inspection of all pine stock intended for planting; destruction of all gooseberry and currant bushes in infected districts. The November issue of *American Forestry* calls attention to the progress of the disease and prints a request for public aid in combating it. In the same journal Spaulding and Hartley give an interesting popular

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article on "Safety First in Tree Planting." Notable invasions of parasites affecting agricultural plants and forest trees are mentioned, general movements of parasites from district to district within the United States are discussed, and preventive measures are suggested.

J. G. BROWN.

Mr. Raphael Zon has contributed a paper to the October number of *The Geographical Review* on the timber resources of South America, accompanied by a map showing the regions from which the leading timber trees are secured. South America is now importing North American timber instead of developing its own timber resources. The reasons for this are the scarcity of valuable trees which occur in pure stands and the expensiveness of all lumbering operations. The principal trees of commercial importance in South America at the present time are Parana pine, Spanish cedar, both chiefly cut in southern Brazil, Quebracho, a source of tannin, and Greenheart, used in building ships and docks.

The third annual Report of the Botanical Office of British Columbia has been made by the Provincial Botanist, Mr. J. Davidson. One of the principal pieces of exploration carried out during the past year was in the Skagit Valley. The vegetation of this region is described and illustrated, and a list of its plants is given. Transitional features are shown between the humid conditions of the coast and the relatively dry conditions of the unforested interior.

The Botanical Society of Washington has elected the following officers for the ensuing year: President, Mr. T. H. Kearney; Vice-president, Mr. Edgar L. Brown; Recording Secretary, Mr. Charles E. Chambliss; Corresponding Secretary, Dr. H. L. Shantz; Treasurer, Mr. F. D. Farrell. Mr. A. S. Hitchcock was nominated by the Society for the office of Vice-president of the Washington Academy of Sciences.

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CONTAINING

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The absorption of salts was also less from the solutions containing vanillin than from their controls without vanillin. The absorption of each nutrient element for each culture is given in the table. Considering all the cultures, the phosphate absorption was reduced 21%, the nitrate 10%, and the potash 33%. The absorption of nitrate was less interfered with by the vanillin than either phosphate or potassium.

The results with cowpeas are in harmony with those with wheat seedlings where it was shown that the harmfulness of vanillin was very slight in solutions high in nitrate content, and that its effect was less in cultures composed principally of nitrate than in cultures composed principally of phsophate or potassium.[3] The roots of plants have an oxidizing power which is increased by nitrate fertilizers.[4] Vanillin is changed or even destroyed by oxidation.[5] Thus this compound when used in nutrient solutions composed of a high per cent of nitrates is probably changed and does not remain as such to have its effect on plant growth.

EFFECT OF MANGANESE ON THE ACTION OF VANILLIN AND SALICYLIC ALDEHYDE

The effect of manganese on the harmfulness of salicylic aldehyde was studied in an experiment growing wheat plants in distilled water. The wheat seedlings were grown in culture jars holding 250 cc. of pure distilled water. The plants grew for twelve days. The results are given in table 2.

As seen from the green weight figures in the table, the salicylic aldehyde was harmful in distilled water in amounts of 5 and 10 parts per million. Manganese sulphate in amounts of 1, 5 and 10 parts per million of manganese overcame its effect partly with the lower concentration and entirely with the larger amount. Its influence is shown nicely in the cultures shown in figure 2.

[3] Schreiner, O., and Skinner, J. J., The toxic action of organic compounds as modified by fertilizer salts. Bot. Gaz. **54**: 31. 1912.

[4] Schreiner, O., and Reed, H. S., The rôle of oxidation in soil fertility. U. S. Dept. Agr., Bur. Soils Bul. 56. 1909.

[5] Schreiner, O., and Reed, H. S., Jour. Amer. Chem. Soc. **30**: 85. (1908).

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A similar experiment growing wheat seedlings in distilled water was made, using vanillin in amounts of 100 parts per million. In both this and the former experiment the plants were grown for twelve days. The effect of the manganese on the action of vanillin is shown in the green weight figures in table 3.

TABLE 2

Effect of manganese sulphate on the action of salicylic aldehyde in distilled water

TREATMENT	GREEN WEIGHT
	grams
Distilled water	1.37
5 p.p.m. salicylic aldehyde	1.18
5 p.p.m. salicylic aldehyde + 1 p.p.m. Mn	1.32
5 p.p.m. salicylic aldehyde + 5 p.p.m. Mn	1.32
5 p.p.m. salicylic aldehyde + 10 p.p.m. Mn	1.50
10 p.p.m. salicylic aldehyde	0.87
10 p.p.m. salicylic aldehyde + 1 p.p.m. Mn	1.04
10 p.p.m. salicylic aldehyde + 5 p.p.m. Mn	1.57
10 p.p.m. salicylic aldehyde + 10 p.p.m. Mn	1.45
1 p.p.m. Mn	1.42
5 p.p.m. Mn	1.59
10 p.p.m. Mn	1.57

TABLE 3

Effect of manganese sulphate on the harmful action of vanillin in distilled water

TREATMENT	GREEN WEIGHT
	grams
Distilled water	2.18
100 p.p.m. vanillin	1.60
100 p.p.m. vanillin + 1 p.p.m. Mn	2.03
100 p.p.m. vanillin + 5 p.p.m. Mn	1.90
1 p.p.m. Mn	2.20
5 p.p.m. Mn	2.24

The harmful effect of vanillin was here also partly overcome by manganese used in small amounts. The oxidizing power of the plant roots was determined in the different culture solutions by the method described in Bulletin 56, Bureau of Soils,[6]

[6] Schreiner, O., and Reed, H. S., The role of oxidation in soil fertility. U. S. Dept. Agr., Bur. Soils Bul. 56. 1909.

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and Bulletin 42 of the U. S. Department of Agriculture.[7] The oxidation was lessened in the vanillin culture but was increased in the solutions where manganese was used, which is in harmony with the growth in these solutions.

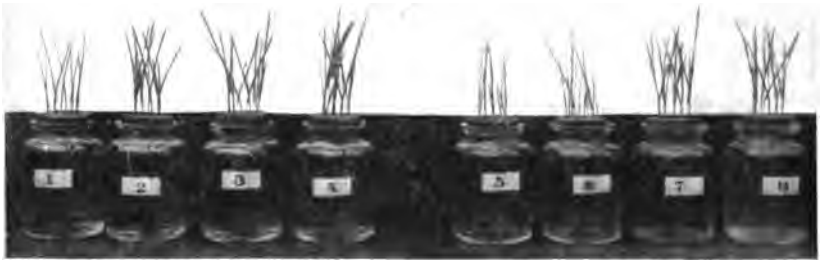

Fig. 2. Wheat seedlings in solutions of salicylic aldehyde without and with manganese sulphate. (No. 1, Salicylic aldehyde 5 p.p.m.; No. 2, Same + 1 p.p.m. Mn; No. 3, Same + 5 p.p.m. Mn; No. 4, Same + 10 p.p.m. Mn; No. 5, salicylic aldehyde 10 p.p.m.; No. 6, Same + 1 p.p.m. Mn; No. 7, Same + 5 p.p.m. Mn; No. 8. Same + 10 p.p.m. Mn.)

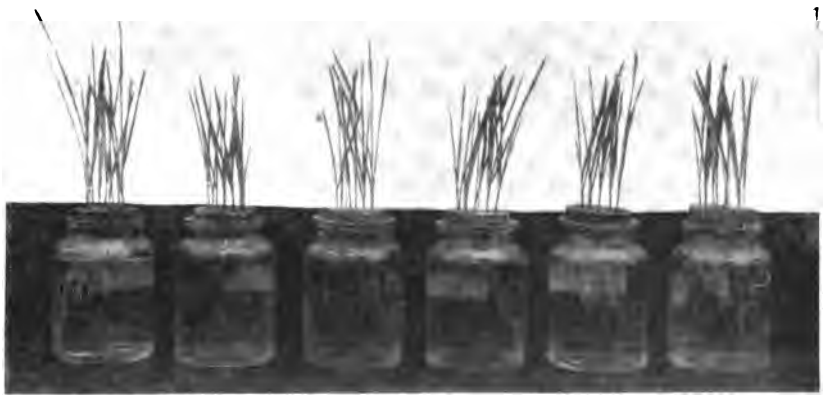

Fig. 3. Wheat seedlings in solutions of vanillin without and with manganese sulphate. (No. 1, Distilled water; No. 2, Vanillin 100 p.p.m.; No. 3, Same + 1 p.p.m. Mn; No. 4, Same + 5 p.p.m. Mn; No. 5, manganese sulphate 1 p.p.m.; No. 6, manganese sulphate 5 p.p.m.).

[7] Skinner, J. J., and Sullivan, M. X., The action of manganese in soils. U. S. Dept. Agr. Bul. 42. 1914.

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Manganese increases the oxidizing power of plants in certain soil extracts[8] as will be as increases the oxidation of certain soils.[7]

In another paper will be given experiments bearing on the effect of manganese in soils to which vanillin and salicylic aldehyde were added. It is there shown that manganese destroyed their effects to a certain extent. All these results point to the fact that manganese through stimulating oxidation can aid in the destruction of such harmful organic substances as aldehydes capable of ready oxidation.

[8] Schreiner, O., Sullivan, M. X., and Reed, H. S., Studies in soil oxidation. U. S. Dept. Agr., Bur. Soils Bul. 73. 1910.

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BOOKS AND CURRENT LITERATURE

FACTORS INFLUENCING NITROGEN FIXATION.—From the Virginia Agricultural Experiment Station has recently appeared another valuable article in the series of studies of the bacterial flora of the soil.[1] The object of the experiments reported in this paper was to determine the importance of various factors that influence the nitrogen fixing power of soil bacteria. Among the factors mentioned are soil moisture, humus content, toxic materials, and effect of salts.

In determining the influence of moisture content, soils which had been tested for nitrogen fixing power, and from which *Azotobacter* had been isolated, were stored in glass jars for twelve to eighteen months when they were practically air dry. Qualitative examinations were then made with the result that *Azotobacter* was found in only four of twenty-five soils from which it had previously been isolated. The moisture content was now increased to 20% and the soils incubated at 28° for three weeks, when tests showed that *Azotobacter* was present in only three of a number of soils in which it had previously been found. The evidence points to a deterioration of *Azotobacter* as a result of drying. In another set of experiments, soils stored in the laboratory for fifteen months lost 24 to 43% of their original nitrogen fixing power, and it is suggested that in the light of the experiments previously mentioned this represents in a large measure the loss due to the lessened vitality of *Azotobacter*. The effect of drying, as shown by the decreased power to fix nitrogen, became evident in some soils in ten days to two weeks, yet after fifteen months other soils showed considerable nitrogen fixing power. This suggests that some nitrogen bacteria are much less affected than *Azotobacter* by decrease in the moisture content of the soil. Toxic substances, which have been regarded by some plant physiologists as the cause of much if not all soil sterility, evidently have but little influence on nitrogen fixing bacteria, for cultures in extracts of sterile soils and control cultures were about equally efficient. Addition of lime to soils of optimum water content and fair nitrifying power stimulated nitrogen bacteria

[1] Williams, Bruce. Some Factors Influencing Nitrogen Fixation and Nitrification. Bot. Gaz. **62**: 311–317. 1916.

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to greater activity, but soils lacking nitrifying power failed to respond to liming, results "contributory to the fact that the nitrifying flora of the soil cannot be developed merely by the use of lime in the absence of other factors more fundamental." Two per cent mannite appeared to be toxic, for no formation of nitrates occurred in cultures to which it had been added.

In the opinion of the reviewer these interesting and valuable studies might be repeated with profit by some of the agricultural experiment stations in the dry-farming region of the West.—J. G. BROWN.

ORANGE RUSTS OF RUBUS.—Announcement was made by Kunkel (Bull. Torr. Bot. Club, 40: 361–366, 1913) about three years ago of the fact that the aeciospores of *Caeoma nitens* Burrill germinate by the production of a promycelium and sporidia. A recent paper[1] clears up the problem of the relationship of *Gymnoconia interstitialis* (Schlecht) Lagerh., which was left unsolved in the earlier report. Two forms of orange rust are found to occur within the United States and the *Caeoma* stage of each of them is morphologically alike. The germination of the one, *Caeoma nitens*, however, is teleutoid and of the other, aecidioid. The former is thus a short cycled rust like *Endophyllum*, whereas the other is the aecial stage of *Gymnoconia interstitialis*, as shown by germination studies, inoculations, and collections. The short cycled form appears to be the one so destructive to cultivated species of *Rubus* in this country.—FREDERICK A. WOLF.

[1] Kunkel, L. O. Further studies of the orange rusts of Rubus in the United States. Bull. Torr. Bot. Club 43: 559–569, figs. 5, 1916.

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NOTES AND COMMENT

Three numbers have appeared in the second volume of Physiological Researches, as follows: The Cryoscopic Constants of Expressed Vegetable Saps, as Related to Environmental Conditions in the Arizona Deserts, by J. Arthur Harris and John V. Lawrence, with the coöperation of R. A. Gortner; Further Studies of Foliar Transpiring Power in Plants, by A. L. Bakke and B. E. Livingston; An Analysis of the Causes of Variations in the Transpiring Power of Cacti, by Edith B. Shreve. The fourth number, now in press, is by Forman T. McLean, and describes his work on the correlation between plant growth and climatic conditions in Maryland.

Mr. L. S. Murphy has prepared a bulletin on the Forests of Porto Rico (U. S. Agr. Dep. Bull. 354), with special reference to the probable character of the original forests and the possibility of increasing the present forest production. Porto Rico now has a rural population of 260 per square mile, and uses three times as much wood per annum as is produced by its forested areas. There is a small body of rainforest in the Luquillo Mountains, which was formerly surrounded by a low deciduous type of xerophytic forest, occupying most of the lower portions of the island.

The H. W. Wilson Company, of White Plains, N. Y., is publishing an Agricultural Index, which lists and classifies the articles in all state and national agricultural bulletins and in about sixty magazines and journals. The index comprises titles in scientific, practical, and educational subjects in every branch of agriculture, horticulture, and forestry. The charge to libraries is determined by the number of indexed magazines for which the library subscribes.

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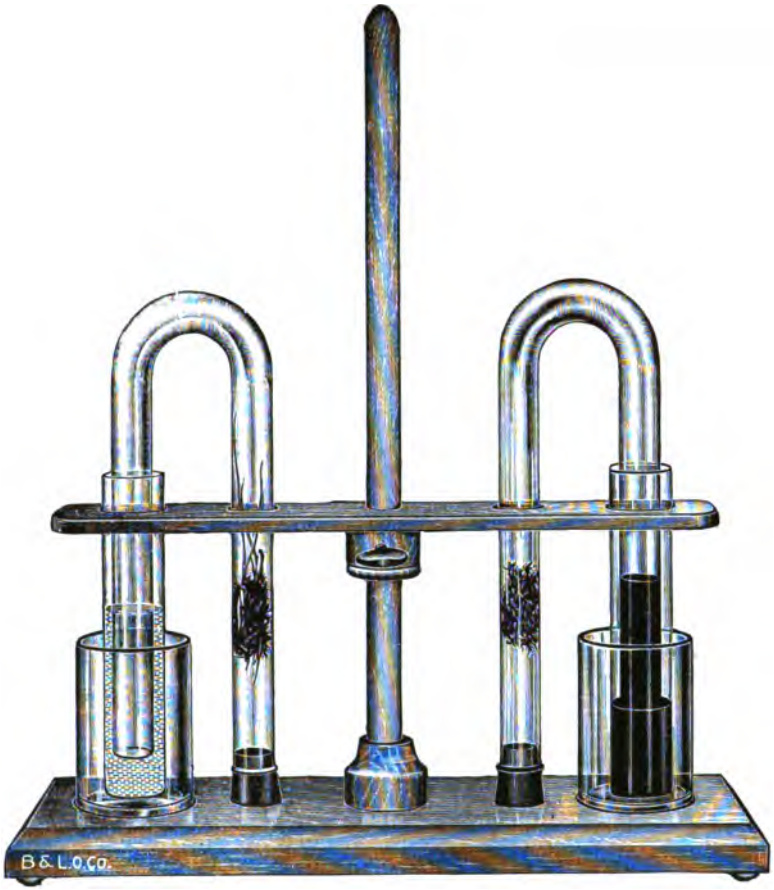

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